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IN
GENETICS

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EXPERIMENTS IN GENETICS

BY

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PREFACE

AFTER thirty years it may serve a useful purpose to collect into one volume the more important papers reporting the results of my experiments and researches in the Genetics of Plants, Animals and Man carried out from 1894 to 1924.

These reports are for the most part scattered in the Transactions and Proceedings of various scientific societies some of which are not very accessible, while others, published by certain specialist societies are, judging from my correspondence, difficult to obtain or to consult.

The collected Papers I—XXXVIII, published from 1897 to 1925, are arranged in chronological order with the idea of illustrating as far as possible the natural development of the Science of Genetics during the last thirty years.

The first four Papers I—IV (1897—1900) record my early experiments in the hybridisation of orchids made before the dawn of the Mendelian era. These were inspired by the reading of Darwin's *Fertilisation of Orchids* in 1894, and in the light of Mendel these old experiments take on a new importance and significance.

Papers V—XXV (1900—1911) report the results of Mendelian experiments with various genera of plants and animals together with Mendelian researches in Horses and in Man. These constitute an experimental demonstration of the Mendelian Principles of Heredity.

Papers XXVI—XXXVI (1911—1921) deal mainly with the problems of the application of the principles of Mendelism and Genetics to the Breeding of Plants and Animals, and also to some extent with the question of Eugenics in Man.

Paper XXXVII (1921) gives a brief historical account of the origin of the Moss-Rose mutations.

The last Paper XXXVIII (1925) presents a more advanced phase of Genetics in which the ever pressing problem of the Evolution and Origin of Species is attacked in a new way by means of an intensive study of the chromosomes and characters in the polymorphic genus *Rosa*.

It will be observed that no papers appeared between 1913 and 1921, owing to my absence on military service. It is regrettable to have to record such a break in the continuity of the experiments which had been carried on at Burbage continuously from 1894 to 1914.

It is deplorable to have to record that owing to the War the whole of my genetic experiments came to an untimely end with the solitary exception of the experiments with *Rosa* which fortunately were preserved almost intact. All the other experimental plants and animals disappeared during the War in divers ways. Some perished from lack of attention while others were sacrificed for food production. Some of the experimental horses served in the army and made excellent chargers. Fortunately the experiments with poultry were well advanced when the War broke out and they were carried on in my absence by the recorder, Mr J. B. Perkins, until he was called up for service in 1916, so that after the War it was found possible to report some definite, though necessarily incomplete, results from the data accumulated. (See Papers XXXIV—XXXVI.)

Owing to the War, the publication of this book has been considerably delayed, since the collected papers up to 1913 were already in the University Press at Cambridge when the War broke out and publication became impossible for a time. Now that publication is possible, I take the opportunity of bringing the collection up-to-date by including later papers published or prepared since the War.

For permission to republish the papers and articles in this book, and for the reproduction of many of the illustrations, my best thanks are due to the Presidents and Councils of the Royal Society, the Linnean Society, the British Association for the Advancement of Science, the Royal Horticultural Society, the Société Nationale d'Horticulture de France (Paris), the Horticultural Society of New York, the Eugenics Education Society, the National Sweet Pea Society, the National Utility Poultry Society, the Leicester Literary and Philosophical Society, the Naturforschenden Vereines in Brünn, and to the Editors and Publishers of *Nature*, *The Times*, *The Gardeners' Chronicle*, *The Orchid Review*, *The Orchid World*, *The National Poultry Journal*, *The Bloodstock Breeder's Review*, *The Mendel Journal*, to Messrs. Williams and Wilkins of the Waverley Press, Baltimore, U.S.A., and the Publication Committee of the 2nd International Congress of Eugenics, New York City.

My best thanks are also due to the following, who in various ways have given me valuable assistance:—Dr W. Bateson, Sc.D., F.R.S.; Professor Sir Rowland Biffen, M.A., F.R.S.; Colonel C. J. Bond, C.M.G., F.R.C.S.; Miss M. S. G. Breeze, B.Sc.; Mr F. T. Brooks, M.A., F.L.S.; Mr E. A. Bunyard, F.L.S.; Mr J. W. Capstick, O.B.E., M.A.; the late Canon Carew-Hunt, M.A.; Professor W. E. Castle; Mr F. J. Chittenden, F.L.S.; Professor C. Correns; Professor L. Cuénot; the late Rev. W. H.

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C. C. H.

TRINITY COLLEGE,
CAMBRIDGE.

May, 1925.

CORRIGENDA

- pp. 1, 2, 4, 32, 39. *For* Exul *read* exul.
- p. 20. *For* O. × cirrhosum *read* O. cirrhosum.
- p. 30. *For* Dominri *read* Dominii.
- p. 31. *For* Schomburgia *read* Schomburgkia.
- pp. 58, 62. *For* Fairieanum *read* Fairrieianum.
- p. 60. *For* orchideous *read* orchidaceous.
- pp. 63, 68, 80, 82, 88, 89, 90. *For* Orchideæ *read* Orchidaceæ.
- p. 75. *For* amæna *read* amœnum.
- p. 75. *For* delicatulum *read* delicatum.
- p. 79. *For* Carophylleæ *read* Carophyllaceæ.
- p. 79. *For* Scrophularinæ *read* Scrophulariaceæ.
- p. 79. *For* Amaryllideæ *read* Amaryllidaceæ.
- p. 80. *For* Onagrarieæ *read* Onagraceæ.
- p. 216. *For* Crève-cœur *read* Crève-Cœur.
- p. 274, l. 11 from end. *After* eyes *delete comma.*
- p. 359. *For* Ruëmker *read* Rümker.
- p. 361. *For* (Varleyata) *read* (varleyata).
- p. 505. *For* (Hamburg Mode) *read* (Hamburgh Mode).

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I

CURIOUS CROSSES

*First Note*¹.

Early in 1897, for the sake of experiment, I determined to try a few outlandish crosses, and I have been surprised to find that out of eight crosses made between different—in several cases very distinct—genera, only one failed to set, and that was the reverse cross of one which appears to have “taken well.” The following is a list of the crosses made, with the dates, and the results up to the present:

Lycaste Skinneri ♀ (fig. 1) × *Lælia anceps Sanderiana* ♂ (fig. 2).

Crossed 15th February, 1897; a healthy-looking pod, 5 inches in girth.

Lælia anceps Sanderiana ♀ × *Lycaste Skinneri* ♂. Crossed 15th February, 1897; did not take (the reverse cross of the preceding).

Lycaste Skinneri ♀ × *Lælia* (*Brassavola*) *glauca* ♂. Crossed 16th March, 1897; a good-looking pod, 4 inches in girth.

Ada aurantiaca ♀ × *Lælia* (*Brassavola*) *glauca* ♂. Crossed 16th March, 1897; pod swelled slightly, but gradually faded.

Cypripedium Calceolus ♀ × *Phragmipedium* (*Selenipedium*) × *Sedenii candidulum* ♂. Crossed 18th March, 1897; a well-formed pod over 1 inch in girth.

Paphiopedium (*Cypripedium*) *Exul* ♀ × *Cypripedium Calceolus* ♂. Crossed 16th April, 1897; a fine-looking pod, over 1¼ inches in girth.

Angræcum sesquipedale ♀ (fig. 3) × *Lælia purpurata* ♂ (fig. 4). Crossed 9th May, 1897; pod forming rapidly, already 3½ inches in girth.

Cattleya Mossiæ ♀ × *Angræcum sesquipedale* ♂. Crossed 9th May, 1897; pod forming, now 1¼ inches in girth.

Perhaps some may think me rather premature in putting these crosses on record, considering the short time that has elapsed since their pollination, and especially as it yet remains to be seen whether these healthy-looking pods will produce good seed. On the other hand, the above list may possibly encourage some to attempt other curious crosses, hitherto hardly dreamed of in the philosophy of Orchid breed-

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ing—crosses which might lead to results at which the Orchid world would wonder, and which would, at the same time, throw a light on the dark mysteries of evolution.

*Second Note*¹.

In June last I recorded a few curious generic crosses, which, judging from the healthy appearance of the pods at that time, seemed likely to succeed. Since then four of those pods have finished their course, two of them having come to an untimely end, while the other two have ripened and produced good seeds, as the following notes will show.

On 18th March, 1897, *Cypripedium Calceolus* was crossed with the pollen of *Phragmipedium* × *Sedenii*, and the pod, after passing through the usual stages of growth, ripened and opened naturally on 15th August (150 days after pollination). A careful examination of the interior of the pod showed thousands of shrivelled ovules, among which, here and there, were 166 plump and well-developed seeds. These latter were a shiny dark brown colour, and under the microscope a small dark egg-shaped spot (embryo) was discerned in the middle of each seed, and grains of green coloured matter (chlorophyll) were distributed all over the interior of the seed. They were almost transparent, and were covered with a finely-netted skin. They varied considerably in shape, some being bent up at the ends, others quite straight, some keel-shaped, others serpentine in outline, but all agreeing in having swollen middles and attenuated ends. Every one of the 166 seeds appeared to be healthy and fertile.

On 16th April, 1897, *Paphiopedium Exul* was crossed with the pollen of *Cypripedium Calceolus*; the seed-pod duly matured and ripened on 18th November (216 days after pollination). An examination of the contents of the pod showed, like the last, a vast number of shrivelled ovules, but in this case there was a much larger proportion of plump, well-developed seeds, these numbering 597 all told. Viewed under the microscope these seeds appeared to be more or less egg-shaped, and being almost opaque were more difficult to examine than the last, being dull dark brown in colour, and covered with a coarsely netted skin, the surface of which was very uneven in colour. The whole of these seeds were plump, and, as far as one could judge, healthy and good.

On 9th May, 1897, *Cattleya Mossiæ* was crossed with the pollen of *Angræcum sesquipedale*. The pod gradually swelled until 18th June

¹ Reprinted from *The Orchid Review*, 1897, Vol. v. pp. 365–367.



Fig. 1. *Lycaste Skinneri* Lindl. var. *alba* Hort.
An albino of the species from Guatemala. Crossed with genus *Lelia* (fig. 2).
(*Orchid World*.)



Fig. 2. *Laelia anceps* Lindl. var. *Sanderiana* Rehb. f.
An albinic form of the species from Mexico. Crossed with genus *Lycaste* (fig. 1).
(*Orchid Revue*.)

(40 days after pollination), when it measured $2\frac{1}{8}$ inches in girth. On this day it commenced to change colour, turning from deep green to pinky green, and then to pinky yellow, and on the 1st of July the pod was quite soft at the base, the upper part nearest the column being still more or less firm, but evidently in a state of decay. A vertical section of the pod and column showed that the pollen tubes had grown down the columnar canal to the length of $2\frac{1}{2}$ inches, and in a few cases had even entered the seed-chamber itself, though they did not appear to have come into contact with the ovules. These latter had developed slightly, but showed no signs of fertilisation.

On the same day *Angræcum sesquipedale* was crossed with the pollen of *Lælia purpurata*. The pod swelled very rapidly until 28th July, when it reached its climax (80 days after pollination). It then measured $4\frac{1}{2}$ inches in girth and began to change colour, and two days afterwards it opened naturally. Inside the pod I could find no trace of a single seed, though it was full of chaff and shrivelled ovules, together with a large number of fine fluffy fibres, or downy threads loosely woven together, completely choking up the middle of the pod along its whole length. After the pod had dried these fibres became quite glossy in appearance, and reminded one somewhat of cotton.

The two remaining crosses, *Lycaste Skinneri* crossed with the pollen of *Lælia anceps* on 15th February, 1897, and *Lycaste Skinneri* crossed with *Brassavola glauca*, on 16th March, 1897, appear to be doing well, and are gradually increasing in size.

I have recently set two pods of *Oncidium incurvum*, crossed with the pollen of *Odontoglossum crispum*, on 11th August, 1897, which appear to be healthy and full of vigour. For the present I think any speculations as to the probable outcome of these curious crosses, however interesting to contemplate, would serve no useful purpose. For not only have the *fertile* seeds to pass through the uncertainties of germination before plants are obtained, but even then they may resolutely refuse to flower, as in the case of many well-known crosses between *Paphiopedium* and *Phragmipedium*, and even if this much desired consummation be reached, there is still the possibility that they may not flower as true hybrids.

Third Note¹.

During the past three years I have been experimenting with generic crosses—more or less outlandish—and thinking that the results might

¹ Reprinted from *The Orchid Review*, 1899, Vol. vii. pp. 13–15.

possibly be interesting to the readers of the *Orchid Review*, I have tabulated the whole of them as follows:

(1) CAPSULES CONTAINING GOOD SEEDS.

- Sophronitis grandiflora* × *Cattleya labiata*. Pollinated Dec. 16, 1895.
Capsule opened Oct. 5, 1896. Seeds germinating.
- Sophronitis grandiflora* × *Lælia anceps*. Pollinated Dec. 16, 1895.
Capsule opened Nov. 10, 1896. Seeds germinating.
- Sophronitis grandiflora* × *Cattleya Schrödera*. Pollinated April 5, 1896. Capsule opened April 10, 1897. Seeds germinating.
- Phragmipedium* × *Sedeni* × *Paphiopedium insigne*. Pollinated Nov. 28, 1896. Capsule opened April 16, 1897. 50 per cent. good seeds.
- Cypripedium Calceolus* × *Phragmipedium* × *Sedeni*. Pollinated March 18, 1897. Capsule opened Aug. 15, 1897. 166 good seeds.
- Paphiopedium Exul* × *Cypripedium Calceolus*. Pollinated April 16, 1897. Capsule opened Nov. 18, 1897. 597 good seeds.
- Paphiopedium Lawrenceanum* × *Phragmipedium* × *Sedeni*. Pollinated May 28, 1897. Capsule opened Dec. 4, 1897. A few good seeds.
- Oncidium incurvum* × *Odontoglossum crispum*. Pollinated Aug. 11, 1897. Capsule opened April 25, 1898. 2 capsules, hundreds of good seeds.
- Paphiopedium insigne* × *Phragmipedium* × *Sedeni*. Pollinated Dec. 13, 1897. Capsule opened Aug. 14, 1898. A few good seeds.

(2) CAPSULES FULLY DEVELOPED, OPENED NATURALLY,
BUT NO SEEDS.

- Lycaste Skinneri* × *Lælia anceps*. Pollinated Feb. 15, 1897. Capsule opened March 10, 1898. A few chaffy ovules.
- Lycaste Skinneri* × *Brassavola glauca*. Pollinated March 16, 1897. Capsule opened March 25, 1898. A few chaffy ovules.
- Cattleya citrina* × *Sophronitis grandiflora*. Pollinated April 14, 1897. Capsule opened Oct. 31, 1897. Many chaffy ovules.
- Angræcum sesquipedale* × *Lælia purpurata*. Pollinated May 9, 1897. Capsule opened July 30, 1897. Full of cottony fibres.
- Paphiopedium insigne* × *Odontoglossum crispum*. Pollinated Nov. 18, 1897. Capsule opened Oct. 8, 1898. A few chaffy ovules.
- Angræcum sesquipedale* × *Vanda tricolor*. Pollinated Jan. 1, 1898. Capsule opened May 25, 1898. Many cottony fibres.



Fig. 3. *Angraecum sesquipedale* Thouars. A native of Madagascar. Crossed with genus *Laelia* (fig. 4).

(*Orchid World*).



Fig. 4. *Lælia purpurata* Lindl.

A native of Brazil. From a photograph of a dark-coloured form which first flowered at Burbage and is apparently synonymous with *L. p. blenheimensis* Hort. Crossed with genus *Angraecum* (fig. 3).

(3) CAPSULES PARTLY FORMED.

- Ada aurantiaca* × *Brassavola glauca*. Pollinated March 16, 1897.
Capsule dropped April 12, 1897.
- Cattleya Mossiæ* × *Angræcum sesquipedale*. Pollinated May 9, 1897.
Capsule dropped July 1, 1897.
- Dendrobium Phalænopsis* × *Odontoglossum nobile*. Pollinated July 12, 1897. Capsule dropped July 20, 1897.
- Epidendrum cochleatum* × *Dendrobium Phalænopsis*. Pollinated July 12, 1897. Capsule dropped August 8, 1897.
- Epidendrum cochleatum* × *Odontoglossum nobile*. Pollinated July 18, 1897. Capsule dropped August 7, 1897.
- Epidendrum cochleatum* × *Odontoglossum crispum*. Pollinated July 25, 1897. Capsule dropped August 9, 1897.
- Epidendrum cochleatum* × *Odontoglossum crispum*. Pollinated August 11, 1897. Capsule dropped August 25, 1897.
- Epidendrum fragrans* × *Odontoglossum crispum*. Pollinated June 29, 1898. Capsule dropped August 3, 1898.
- Cattleya Leopoldi* × *Dendrobium Phalænopsis*. Pollinated July 12, 1897.
Capsule dropped July 24, 1897.
- Epidendrum fragrans* × *Cattleya Mendelii*. Pollinated June 29, 1898.
Capsule dropped Aug. 3, 1898.

(4) FAILED TO SET CAPSULES.

- Lælia anceps* × *Lycaste Skinneri*. Pollinated Feb. 15, 1897. Flower faded in 11 days.
- Brassavola glauca* × *Lælia harpophylla*. Pollinated March 16, 1897.
Flower faded in 8 days.
- Brassavola glauca* × *Sophronitis grandiflora*. Pollinated March 16, 1897. Flower faded in 8 days.
- Dendrobium Phalænopsis* (2 fl.) × *Cattleya Leopoldi*. Pollinated July 12, 1897. Column withered, pollen fresh.
- Paphiopedium insigne* × *Cattleya Bowringiana*. Pollinated Nov. 18, 1897. Pollen dried up, flower fresh.
- Paphiopedium insigne* × *Dendrobium formosum*. Pollinated Nov. 18, 1897. Pollen rotted stigma away.
- Epidendrum fragrans* (2 fl.) × *Dendrobium Phalænopsis*. Pollinated June 28, 1898. Column withered, pollen fresh.
- Epidendrum fragrans* (2 fl.) × *Dendrobium Dearei*. Pollinated June 29, 1898. Column withered, pollen fresh.
- Epidendrum fragrans* (3 fl.) × *Paphiopedium niveum*. Pollinated June 29, 1898. Column withered, pollen decayed.

II

NOTES ON SOME CURIOSITIES OF ORCHID BREEDING¹

During the past few years the number of Orchid hybrids raised by hand has increased by leaps and bounds, and with this increase have come numbers of curiosities and mysteries which seem to baffle us at every turn. Fortunately during the same period much light has been thrown on the actual details of fertilisation, and my object in these notes is to put on record in a concise form a few of these curiosities, and at the same time to view them in the light of recent researches. A careful study of these curiosities suggests the desirability of working through the normal up to the abnormal, and you will perhaps pardon me if before dealing with the extraordinary I give you a brief outline of the ordinary facts of hybridisation, and then I think we shall be better able to deal with "Some Curiosities of Orchid Breeding."

HYBRIDS OF THE FIRST GENERATION.

Hybrids between two distinct species of Orchids are generally intermediate in character between their two parents, and usually are so intermediate as to be quite distinct from either (cf. figs. 5-23).

For instance, the well-known garden hybrid *Cypripedium* × *Leeanum* (fig. 5) is fairly intermediate between its two parents, *C. Spicerianum* (fig. 6) and *C. insigne* (fig. 9), so much so that it is quite distinct from either.

Sometimes one part of a hybrid seems to resemble one parent more than the other; for instance, in *C.* × *Leeanum* the upper sepal of the flower outwardly seems to resemble *C. Spicerianum* more than *C. insigne*; while, on the other hand, the staminode of the flower and the leaves and general habit of the hybrid appear to incline towards *C. insigne* rather than *C. Spicerianum*.

Yet Professor Macfarlane, of the University of Pennsylvania, Phila-

¹ Lecture delivered before the Royal Horticultural Society 12th October 1897. Reprinted from the Society's *Journal*, 1898, Vol. xxi. Pt 3, pp. 442-486.



Fig. 5. × *Cypripedium Leeanum* Rchb. f.
A garden hybrid from *C. insigne* Wallich ex Lindl. (fig. 9) and
C. Spicerianum Rchb. f. (fig. 6).
(*Orchid Review*.)



Fig. 7. \times *Cypripedium Lathamianum* Rehb. f.

A garden hybrid from

Fig. 6. *C. Spicerianum* Rehb. f.

and

Fig. 8. *C. villosum* Lindl.

From a photograph taken at Burbage.



Fig. 10. \times *Cypripedium nitens superbum* Rehb. f.

A garden hybrid from

Fig. 9. *C. insigne* Wallich ex Lindl. var. *Chantini* Raf.

and

Fig. 11. *C. villosum* Lindl.

From a photograph taken at Burbage.

delphia, U.S.A., who has carefully worked out the minute structure of this hybrid, found that even these parts were fairly intermediate in character, though it was not so apparent to the naked eye. ("Minute Structure of Plant Hybrids," *Trans. Roy. Soc. Edin.* 1891, xxvii. Part I. No. 14, p. 245.)

Professor Macfarlane found that the margin and inner surface of the upper sepal of *C. × Lecanum* were both covered with simple and glandular hairs side by side, while the parent *C. Spicerianum* had glandular hairs only, and the parent *C. insigne* simple hairs only; further, the hybrid had the ruby hairs of *C. Spicerianum* along the midrib, though less in number, and the glabrous spots of *C. insigne*, but reduced in size and number. (*Id.* p. 247.)

Again, the staminode of *C. × Leea* in colour and roughness of surface outwardly resembles that of *C. insigne*, there being no trace apparently of the purple and white smooth staminode of *C. Spicerianum* (except the slightly modified shape), but a section clearly showed a structure intermediate between both parents, and a reduction by one half in the size of the *protuberances* and in the number of hairs. (*Id.* p. 248.)

Further, though the leaves and the general habit of the hybrid seem to incline towards the parent, *C. insigne*, yet Professor Macfarlane observed that their inner structure was fairly intermediate between both parents; curiously enough, in the average number of stomata and epidermal cells the upper surface of the leaf inclined considerably towards *C. insigne*, while the under surface slightly leaned towards *C. Spicerianum*. (*Id.* p. 245.)

Other hybrids have been examined minutely by Professor Macfarlane, and all have more or less given the same results, which thus show that the inner tissues as well as the outer characters, if carefully observed, are found to be fairly blended between the two parent species.

A plate prepared by Professor Macfarlane shows this very clearly. The beautiful colour of the hybrid *Masdevallia × Chelsoni* and its two parents, *M. Veitchiana* and *M. amabilis*, is due in a large measure to the crimson hairs which are distributed thickly over the surface of the sepals. When magnified, the hairs of *M. Veitchiana* are seen to be globular in shape, while those of *M. amabilis* are cone-shaped; on the other hand, the hairs of the hybrid are club-shaped, being intermediate between the two and distinct from both. (*Id.* p. 242, Plate VII., figs. 3, 4, and 5.)

True hybrids between two distinct species are not found to differ

from one another more than individuals of a species are wont to do. Thus *Cypripedium Spicerianum* crossed with *C. insigne* always produces *C. × Leeanum*, whether from the same seed-pod or from different seed-pods, and can never be mistaken for anything else. Nor does it matter which way the cross is made, whether *C. Spicerianum* be used as the seed parent (*C. Spicerianum* ♀ × *C. insigne* ♂) or whether *C. insigne* be used as the seed parent (*C. insigne* ♀ × *C. Spicerianum* ♂); no matter when or where they may be crossed (if proper fertilisation takes place), they always produce *C. × Leeanum*. Hence we see the great importance of having one recognised name, and one only, for all hybrids between the same two species. (See my notes on "Nomenclature of Orchids," *Orchid Review*, 1896, iv. p. 165.) Naturally, like species, hybrids from the same two species vary considerably in minor details, especially in colour and size, which though of little importance to the systematic botanist, yet make or mar a plant in the eyes of the Orchid grower; and it is very necessary from an artistic and commercial point of view that these colour and size variations should, when distinct, bear a special name; but it is equally necessary that this name should be a varietal one only, and not a specific one, in order that the scientific nomenclature of hybrids be not tampered with.

These variations in hybrids of the first generation are generally found to correspond with the varieties of the parent species, and to have the same limited range. For instance, the varieties of the hybrid *C. × Leeanum* are almost innumerable; but so are the varieties of one of its parents, *C. insigne*; and it is generally found that if the particular variety used as a parent be a constant one, it will affect the hybrid offspring in a particular way. For instance, to take two extreme cases, *C. Spicerianum* ♀ × *C. insigne* *Sanderæ* ♂ (*a very light form* of *C. insigne*), raised by Mr Seden for Messrs Veitch & Sons, of Chelsea (fig. 59), produced *C. × Leeanum* "*Prospero*," *a very light form* of *C. × Leeanum*. (*Orch. Rev.* v. p. 65.) Again, *C. Spicerianum* ♀ × *C. insigne* *Wallacei* ♂ (*a heavily and densely spotted* variety of *C. insigne*), raised by M. Jules Hye, of Gand, Belgium, produced *C. × Leeanum* *Albertianum*, *a heavily and densely spotted* variety of *C. × Leeanum*. (*Cogn., Dict. Icon. des Orch.* February 1897, Cyp. hyb. pl. 3A.) If the particular variety used be not a constant one, many variations will be produced even from one seed-pod.

A few years ago Mr Chas. Winn, of Selly Hill, Birmingham, showed me a large number of *C. × Leeanum* in flower, which were raised by him from *C. insigne* *Chantinii* (fig. 9) and *C. Spicerianum*. Hardly any two



Fig. 13. \times *Cypripedium Suttoniæ* Rolfe.

A garden hybrid from

Fig. 12. *C. niveum* Reh. f.

and

Fig. 14. *C. Chamberlainianum* O'Brien.

(*Orchid Review*.)



Fig. 16. \times *Dendrobium Schneiderianum* Reh. f.

A garden hybrid out of

Fig. 15. *D. Findlayanum* Parish et Reh. f.

by

Fig. 17. *D. aureum* Lindl.

(*Orchid Review*.)



Fig. 19. \times *Cypripedium Nellie Pitt* ex O'Brien.

A garden hybrid out of

by

Fig. 20. *C. Charlesworthii* Rolfe.

Fig. 18. *C. tonsum* Rehb. f.

(*Orchid Review*.)

plants were alike in colour or spotting, and they also varied in the shape of the upper sepal, some being much more reflexed than others; and one might easily have picked out from this batch of seedlings many well-marked varieties, including the typical *C. × Leeaenum*, *C. × L. superbum* (fig. 61), and *C. × L. giganteum*, to say nothing of intermediate forms and minor varieties. We need not, however, be surprised at this when we learn that one of the parents, *C. insigne Chantinii*, though a well-marked variety, is not a constant one from seed.

Mr W. Grey, for Hon. Erastus Corning, Albany, New York, U.S.A., raised seedlings of *C. insigne Chantinii* fertilised with its own pollen, and produced thirty different varieties from one pod (*Orch. Rev.* II. p. 227); so that *C. insigne Chantinii* is evidently a variety "with a past," and when crossed with *C. Spicerianum* its history tends to repeat itself, and many forms of *C. × Leeaenum* are the result.

On the other hand, we know that some varieties are quite constant from seed, for Mr Norman Cookson, of Wylam-on-Tyne, fertilised *C. Lawrenceanum Hyeaenum* (a so-called "albino") (fig. 58) with its own pollen; and of the plants raised therefrom three have already flowered true to the parent variety (*Gard. Chron.* January 16, 1897, p. 37, fig. 8), so that *C. L. Hyeaenum* is evidently a variety "without a past": it consequently breeds true to colour, and would no doubt set its peculiar mark on its offspring if crossed with another species, in the same way as we have seen that *C. insigne Sanderæ* has done in *C. × Leeaenum* "Prospero," and *C. insigne Wallacei* in *C. × Leeaenum Albertianum*¹.

REVERSE CROSSES.

It sometimes happens (especially when only a few plants have been raised of a particular cross) that the reverse cross (*B ♀ × A ♂* instead of *A ♀ × B ♂*) produces hybrids differing in variety from the original cross, and many people have immediately come to the conclusion that this variation was due to the parents being reversed. But, as can easily be perceived, this does not necessarily follow. *Post hoc* certainly, but *ergo propter hoc* by no means. This palpable fallacy is further exposed when we find that many reverse crosses are not at all different; for instance, Mr Seden, for Messrs Veitch & Sons, crossed *C. Schlimii ♀* with *C. longifolium ♂* and *C. longifolium ♀* with *Schlimii ♂*, which produced the well-known hybrid *C. × Sedenii*. "No perceptible

¹ Cf. later experiments which show that true-breeding albinos may be carrying various colour and pattern factors. (Note added 1914.)

difference was observed between the plants raised from the two separate crosses: they agree in habit, foliage, structure, and colour of flower; in fact in every particular." (Veitch, *Man. Orch.* Part x. p. 143.) Instances like this completely dispose of the theory that reverse crosses are intrinsically different¹.

A careful inquiry into the variations occasionally seen in reverse crosses shows that they are mostly due to a different variety being used as a parent in each case, the offspring varying accordingly.

In the few cases in which the same variety has been used in each case the variation is no doubt due to the variability of the parent's history, which is duly handed on to the offspring, and if but one or two plants be raised from each cross the chances are that the survivors will be widely different.

Theoretically, if every possible variety could be raised between $A \text{ ♀} \times B \text{ ♂}$ and between $B \text{ ♀} \times A \text{ ♂}$ on comparison the varieties of the former would be found to correspond with the latter exactly. It would be difficult to demonstrate this in Orchids, because out of thousands of individual seeds in a pod so few plants are raised which arrive at the flowering age; but it has been demonstrated in plants other than Orchids by the experiments of careful observers. (Kerner and Oliver, *Natural History of Plants*, II. p. 557.)

To sum up the ordinary facts of *hybridisation* in Orchids:

(1) Hybrids of the first generation between two distinct species are generally intermediate between their parents.

(2) This applies to their inner structure as well as to their outward characters.

(3) They are so far intermediate between their parents as to be quite distinct from either.

(4) All hybrids between the same two species are specifically alike, but like species differ in varietal characters.

(5) These varietal differences are found to correspond with the varietal differences in the parent species.

(6) Whether these varietal differences are handed down truly from the species to the hybrid depends upon the history of the variety; if constant it will hand it on truly, if variable it will hand it on as variably.

(7) There is no intrinsic difference in reversed crosses.

¹ Recent experiments with other plants and animals show that some reverse crosses certainly are intrinsically different. It is possible that similar cases may yet be found in Orchids. (*Note added 1914.*)



Fig. 21. *Cattleya bicolor* Lindl.

From Brazil with its local subspecies *C. Grassii* Kränzl. from Rio de Janeiro.

♀ parent of fig. 22.

(*Orchid Review*.)

POLLINATION AND FERTILISATION.

Having ascertained the ordinary results of the hybridisation of two distinct species, it will perhaps clear the way *still further* if we briefly follow out the inner details of pollination and fertilisation, having special regard to recent researches and observations. So far as I know, the most recent work that has been done in Orchids, in regard to the processes of fertilisation, was carried out by Mr Harry Veitch, F.L.S.¹, 1885-87, the results of which were published in the *Journal of the Linnean Society*, vol. xxiv. No. 163, p. 395 (also in Veitch's *Manual of Orchids*, Part x. p. 83); and I am much indebted to Mr Veitch for his invaluable observations. Mr Veitch followed out the inner processes from pollination to fertilisation in *Cattleya Mossiae* pollinated with its own pollen. The pollen masses were applied in the usual way. Two days afterwards the flower faded and the pollen masses began to break up into groups of grains and became thoroughly mixed up with the sticky fluid of the stigma, and from some of the grains short tubes were already pushed out. After six days the pollen tubes had largely increased in numbers, and the longest had reached the base of the column, having worked their way down the duct leading through the middle of the column from the stigma to the seed-chamber or ovary. During this time a wonderful change had taken place in the ovary, or *seed-pod*. Before pollination it was circular in shape; fourteen days later it was triangular and swollen; and at the end of thirty days its walls were still more swollen, and the ovules, the future seeds, were gradually developing into shape and form, though there were as yet no signs of fertilisation. At the end of thirty days the pollen tubes had entered the ovary, and were pushing down along its walls by the side of the placentas which bore the ovules. After fifty-five days the pollen tubes had reached the bottom of the ovary, and were all among the ovules in countless numbers, but no signs of fertilisation could be traced. Seventy-five days after pollination Mr Veitch found the tips of the pollen tubes in contact with the opening leading into the ovule (micropyle), and at this time actual fertilisation began to take place, changing the ovules into seeds.

So far back as 1863 Dr Hildebrandt made observations in the Botanic Gardens at Bonn on the processes of fertilisation in Orchids, somewhat similar to Mr Veitch, but in different genera. (Mohl and Schlechtendal, *Botanische Zeitung*, 1863, Nos. 44 and 45.) Dr Hildebrandt found that the period between pollination and fertilisation varied considerably in

¹ Now Sir Harry Veitch, F.L.S., V.M.H. (*Note added 1914.*)

different Orchids: the period in *Dendrobium nobile* he found to be about 120 days, *Phaius grandifolius* 60 days, *Cypripedium insigne* 120 days, while in hardy terrestrial Orchids, *Listera ovata*, *Neottia nidus-avis*, and *Orchis pyramidalis*, the period was but 8 to 9 days, and *Gymnadenia conopsea*, *Orchis morio*, and *O. maculata* about 14 days. As far as I know, no one has carried actual observations in the fertilisation of Orchids beyond this stage, owing, no doubt, to the fact that the ovules of Orchids being so minute, the further processes would be extremely difficult to follow. Yet there can be little doubt that the further details of fertilisation in Orchids (in common with those already observed) are much the same as in other flowering plants. Indeed, the ultimate processes of fertilisation seem to be much the same in all forms of life. Professor Strasburger and others have worked out the details of fertilisation with marvellous precision in a plant of the genus *Ornithogalum* (Star of Bethlehem), which belongs to the Liliaceæ order, a family closely allied to Orchids. Professor Strasburger observed (Kerner and Oliver, *Natural History of Plants*, II. p. 416) that the pollen grain contained one or two germ cells, which were made up of a nucleus surrounded by a small portion of naked protoplasm. One of these germ cells, or pollen cell, as we may conveniently call it, is carried along near the tip of the pollen tube as it gradually lengthens, and eventually is discharged from the tube through the opening of the ovule into the embryo-sac. Having reached this, the pollen cell at once makes for the egg cell contained therein, and, being many times smaller than the egg cell, enters into it, the nucleus of the pollen cell uniting with the nucleus of the egg cell, the outcome being a fertilised egg cell which in due time becomes the living embryo of the seed. In this way, by the union of the pollen cell of the father with the egg cell of the mother, a new individual is brought into being. We have already seen that characters are handed on equally by both parents; therefore it necessarily follows that in some way or other the determinants of the characters of the father parent are packed up in the small compass of the pollen cell, and those of the mother parent in the egg cell.

We have seen that the pollen cell is many times smaller than the egg cell, consisting as it does almost wholly of nucleus, and we also know that the nuclei of both are fairly balanced in size and contain the same elements. Therefore it naturally follows that in the handing down of characters from one generation to another, the nucleus is the all-important matter, and the surrounding protoplasm, which is so considerable in the egg cell, and so inconsiderable in the pollen cell, has little or

nothing to do with it, though no doubt it serves a useful purpose as a source of food supply for the nuclei and the future embryo.

Recent researches into the nature of the nucleus carried out by Professor Weissmann and others tend to show that the most important elements in its constitution are certain rod-like fibres, looped threads, or round grains called "chromosomes," which change their appearance and their position from time to time, but which nevertheless generally remain constant in number in the same species.

These are present in the nucleus of every cell, but in the germ cells at the time of fertilisation, not only is their position and shape altered, but their number is apparently decreased by one half, and, according to Professor Weissmann's interpretation of the facts in his well-known book, *The Germ-Plasm*, the essence of fertilisation consists in the removal of one half of the nuclear elements from the egg cell of the mother and the replacing of them by an equal number from the pollen cell of the father, and in this way Professor Weissmann accounts for the different phenomena of heredity, reversion, and variation, and endeavours to make clear the many mysteries of inheritance which have puzzled philosophers and naturalists from Aristotle to Darwin.

Later researches seem likely to modify Prof. Weissmann's speculations considerably; but they are not yet sufficiently advanced to form a definite opinion upon, and we must be content to wait patiently for further facts.

I am not aware that the number of nuclear fibres in the cells of Orchids has yet been ascertained, but in the closely allied order of Liliaceæ, in the plant *Lilium Martagon*, M. Guignard has recently observed that while the ordinary cell contained twenty-four nuclear fibres the ripe egg cell had but twelve, apparently showing that it was ready for fertilisation. (M. Guignard, *Compt. Rend.*, May 11, 1891, and "Nouv. Études sur la Fécondation," *Ann. Science Nat. Bot.*, vol. XIV. 1891, p. 163.) So that if we take *Cypripedium* × *Leeanum* as our typical hybrid, we find that its nuclear fibres would be made up one half from its parent *C. Spicerianum* and the other half from its other parent, *C. insigne*; both the parents being pure species their own nuclear fibres would of necessity be pure and true (their ancestors for many generations having been the same species as themselves). These nuclear fibres being, as we have seen, the bearers of the hereditary characters, and determining the building up of the future individual, it is manifest that the hybrid *C.* × *Leeanum* is of necessity an equal blending of its two parent species¹.

¹ In the light of recent demonstrations of the existence of secondary natural hybrids in orchids, this statement now requires some modification. (*Note added 1914.*)

CURIOSITIES.

Occasionally, when two species are crossed, the offspring resemble the mother species only, having no trace of the father species or any other modifying influence. I have found eleven such cases recorded during the past four or five years, and through the kindness of several correspondents and the editor of the *Orchid Review* I am able to give details and particulars of five of these cases.

(1) In May 1891 Mr Reginald Young, of Sefton Park, Liverpool, crossed *Cypripedium barbatum* ♀ with pollen of *C. niveum*. The pod duly ripened, and fourteen plants were raised, of which nine have already flowered. Strange to say, every one of the nine has flowered *C. barbatum*, like the mother species, without a trace of the father parent, *C. niveum*, either in the flowers or leaves. The same cross has been made at least twice before by Messrs Veitch & Sons (*Gardeners' Chronicle*, November 27, 1866), and by Mr W. Bull, of Chelsea, (*Gardeners' Chronicle*, December 20, 1888), both of which produced the true hybrid *C. × Tautzianum*, and in which the father species, *C. niveum*, was strongly represented in both flower and foliage. (See col. fig. *Reichenbachia*, II. t. 65.)

(2) Curiously enough, Mr Young had a somewhat similar experience with another cross. In March 1892 he crossed *C. callosum* ♀ with pollen of *C. × microchilum*, and in due time twelve plants were raised, one of which flowered last May 1897, producing two flowers on one scape, which were practically indistinguishable from the mother species, *C. callosum*.

(3) Some years ago Mr Charles Winn crossed a flower of *C. venustum* ♀ with the pollen of *C. concolor*. Eighteen seedlings were raised, five of which flowered pure *C. venustum* without a trace of *C. concolor*. (Mr Winn did not wait for the other plants to flower, but threw them away.) (*Orchid Review*, III. p. 240; in litt., September 20, 1897.) The same cross had been made before by Messrs Veitch & Sons (*Gardeners' Chronicle*, 1875, p. 804; *Orchid Album*, t. 418) and by Mr Robert Grey for Mr H. Graves, of Orange, New Jersey, U.S.A. (*American Gardening*, March 23, 1895), in both of which the influence of *C. concolor* was very marked, the hybrid being called *C. × Marshallianum*.

(4) In the *Garden*, May 26, 1888, the following note, signed by "W.," appears: "I recently saw in Mr Buchan's garden at Southampton a very good seedling of *Cypripedium* (*longifolium*) *Roezlii*, which had been obtained from the same pod of seed which produced

C. × Sedeni candidulum (*C. (longifolium) Roezlii* ♀ × *C. Schlimii albidum* ♂), evidently proving that all the seeds were not crossed."

(5) Mr George McWilliams, of Whitingsville, Mass., U.S.A., crossed *C. Spicerianum* ♀ with pollen of *C. niveum* ♂, and all of the plants came true *C. Spicerianum*; while at another time Mr McWilliams raised from *C. niveum* ♀ × *C. Spicerianum* ♂ seedlings which showed both parents distinctly. (In litt., September 20, 1897. See *American Gardening*, March 23, 1895.) The same thing too has been observed and recorded in Lilies, Begonias, Strawberries, and other plants; they have been called "False Crosses." (See *Gardeners' Chronicle*, Nov. 10, 1894, p. 568.)

The first question that naturally arises when considering these curiosities is, Are they true hybrids? Were the seeds from which they were raised fertilised by the pollen of the foreign species? If so, why are they not like the intermediate hybrids raised before by others from the same cross, or, as in one case, from the same seed-pod? Now that we know something of the actual details of fertilisation, we can confidently say that these intermediate or true hybrids contained one half the nuclear elements of the mother species and one half of the father species; but can we truly say this of these curiosities? I think not. If these curiosities reproduce the mother species simply, then they must be made up of the nuclear elements of the mother species only. In other words, they must either have been brought into existence by self-fertilisation, or the ovules were developed without the aid of pollen at all, which has been known to occur at least once in an Orchid (Prof. Henslow, *Structure of Flowers*, p. 171), which I will refer to in detail later on.

But all seeds produced without pollen (parthenogenesis) should reproduce the mother plant exactly down to the smallest detail, being nothing more nor less than seed-buds¹. But Mr Young writes: "The plants of my *C. barbatum* ♀ × *C. niveum* ♂ which have now flowered (nine in number), have *not* been exactly alike, either in flower or foliage, nor exactly like the seed parent *C. barbatum*: one plant has flowered with miserably small blooms, much inferior to the parent *C. barbatum*, and this although otherwise the plant appeared healthy and strong.... One or two, I may say two certainly, showed more white in the dorsal sepal than the others, or than the seed parent, but not sufficient to

¹ Recent results suggest that segregation of characters may take place even when seeds are produced without pollen (cf. apogamy and parthenogenesis). (*Note added* 1914.)

show as a *C. barbatum* ♀ *C. niveum* ♂ cross. The foliage, too, varies slightly in substance and markings." (In litt., September 3, 1897.) Mr Young also tells me that the one plant of *C. callosum* ♀ × *C. × microchilum* ♂, which flowered *C. callosum*, is not at all like the mother variety in form. Mr Winn writes to me that the five plants of *C. venustum* ♀ × *C. concolor* ♂ that he flowered "each differed from the other slightly in flower and leaf, but all were *very bad C. venustum*,...while the mother plant was *C. venustum pardinum* variety, a very good form." (In litt., September 20, 1897.) Mr E. O. Orpett, of South Lancaster, Mass., U.S.A., informs me (in litt., September 24, 1897) that Mr McWilliams's *C. Spicerianum* ♀ × *niveum* ♂ seedlings, which "came true *C. Spicerianum*, differed much in themselves, especially in some of them, being but poor forms, while the mother plant was a superb form that I have not seen equalled in other *C. Spicerianum*."

It is therefore evident that these curiosities were not produced without pollen, and we are consequently almost bound to conclude that they were caused by accidental self-fertilisation¹. It is difficult to say exactly how this happened, but Mr Young tells me that at the time (1891) his *C. barbatum* ♀ *C. niveum* ♂ cross was made he did not remove the pollen masses of the seed parent *C. barbatum*; and a short time ago I observed a flower of *C. Spicerianum*, one pollen mass of which had fallen down, and had stuck on the edge of the stigma, with the result that a pod is now set. I have also frequently observed large spiders and smaller flies settled on and crawling over the pollen masses of *Cypripediums*, and it is just possible that the sticky pollen might be carried on to the stigma in this way. With regard to the pollen of the foreign species that was applied by hand, it would no doubt fertilise some of the ovules, but the *self-fertilised* seeds would have a better chance in the struggle for existence, and would grow away quicker and stronger in the earlier stages than would the hybrids, especially those of *C. niveum* and *C. concolor* parentage, which are known to be slow and "miffy" growers; the weaker would have to go to the wall, and the stronger would survive.

¹ In view of the results of recent researches into the nature of apogamy and parthenogenesis one hesitates now to ascribe these false hybrids definitely to accidental self-fertilisation. (Cf. the similar cases of *Zygopetalum*, pp. 35-38, and later.) (Note added 1914.)



Fig. 24. \times *Cyripedium lecanum* Rchb. f.

Showing 15 hybrids of the *First Generation*. Raised at Burbage out of a single capsule of *C. insigne aurescens* (fig. 25) by *C. spicerianum* (fig. 6).



Figs. 25-28. \times *Cyripedium hobartii* Hurst with parents.

Top Row, left to right, *C. insigne* var. *aurescens* Hurst ♀ (fig. 25) \times *C. latianthum* Rchb. f. ♂ (fig. 26), *C. hobartii* var. *giganteum* Hurst (fig. 27). Remainder, *C. hobartii* vars. (fig. 28).

Showing 13 hybrids of the *Second Generation*. Raised at Burbage out of a single capsule of *C. insigne aurescens* by *C. latianthum*. The ♂ parent (fig. 26) is a hybrid of the *First Generation* from *C. villosum* (fig. 8) \times *C. spicerianum* (fig. 6).

HYBRIDS OF THE SECOND GENERATION.

Hybrid Orchids of the second and third generations are well known to differ much in variability from those of the first generation (cf. figs. 24-28). Generally speaking, as we have seen, hybrids of the first generation are uniformly intermediate, having a narrow range of variation (fig. 24); whereas hybrids of the second (figs. 27, 28) and third generations are very variable indeed, having a wide range of variation, sometimes reverting wholly to the parent species or parent hybrid, and occasionally even resembling a collateral hybrid. The more hybrids are crossed with one another the more related they become, and, consequently, reversions to hybrids of the first generation, and indeed to pure species, become more frequent. This of course acts as a reaction to variation¹.

With regard to the nomenclature of hybrids of the second and succeeding generations, it is not necessary—indeed it would not be wise—to give each distinct cross a distinctive name (as should certainly be done in hybrids of the first generation), for it is manifest that with such extraordinary variations and reversions as occur from the same seed-pod in most hybrids beyond the first generation, nomenclature would be reduced to an absurdity by such a system. But each distinct form, if worthy of a name, should be given a popular one, like a Rose or any other florist's flower. It would no doubt be a great convenience to all if such names were made up of one word only, and that a short one. On the other hand, in the interests of science, a careful record should be kept of the pedigree of each plant for future reference.

CURIOSITIES IN SECOND GENERATION HYBRIDS.

One of the most curious results on record in crossing Orchids is that of Mr W. Grey, for Hon. Erastus Corning, at Albany, New York, U.S.A.

Mr Grey crossed *C. × Godefroyæ* ♀ (figs. 29, 30) with pollen of *C. niveum* (fig. 31), and from the same seed-pod is said to have raised *C. concolor* (fig. 32), *C. niveum*, *C. × Godefroyæ*, *C. × G. leucochilum* (fig. 30), *C. × G. pure-white*, *C. bellatulum* (fig. 33), and nearly fifty intermediate forms. (*Orchid Review*, II. p. 227.) At first sight this result appears incredible, but when we remember how closely allied

¹ The discovery of Mendelian segregation some three years later has made it possible to account for these facts in a more definite and precise form. (*Note added 1914.*)

are the two parents in both appearance and structure, not only to one another, but also to *C. concolor* and *C. bellatulum*, we are not so sure that it is impossible. The mother parent, *C. × Godefroyæ*, was formerly thought to be a species; but since it has been raised twice by hand from *C. concolor* × *C. bellatulum*, and all three are known to grow near one another, we must, I think, consider it to be a natural hybrid.

Sir Charles Strickland, Bart., of Hildeney, Malton, Yorkshire, showed at the Royal Horticultural Society's meeting on May 14, 1895, "three plants of *C. concolor* × *C. bellatulum* which closely resembled *C. × Godefroyæ*." One of these plants came into the possession of Capt. Schofield, New-Hall-Hey, Rawtenstall, Manchester, who says that "it would be impossible to separate it from a fine form of *C. × Godefroyæ*." (*Orchid Review*, v. p. 75.) Again, Mr Statter, of Stand Hall, Whitefield, Manchester, showed at the Temple Show of the Royal Horticultural Society, 1897, *C. × concolor* × *C. bellatulum*, which resembled a form of *C. × Godefroyæ* with a yellow ground, and from which it would be difficult to distinguish it." (*Gardeners' Chronicle*, June 5, 1897, p. 418.) We know that *C. concolor* and *C. × Godefroyæ* grow together in South Siam (*Garden*, 1885, p. 342), and that *C. bellatulum* has also been found in the same district (*Ridley Jour. Linn. Soc. Bot.* xxxii. (1896), p. 415), so that it is quite possible for the natural hybrid *C. × Godefroyæ* to result therefrom. The fact too that *C. × Godefroyæ* is only imported in small numbers tends to confirm this. (Cf. footnote on p. 19 and fig. 36 of *C. G. leucochilum*.)

On June 15, 1897, Mr H. Druce, of St John's Wood, showed at the Royal Horticultural Society *C. × "Mrs Druce"* (fig. 34), raised from *C. niveum* ♀ × *C. bellatulum* ♂, "the flower of which resembled *C. × Godefroyæ*." (*Gardeners' Chronicle*, June 19, 1897, p. 411.)¹ We have already seen that *C. concolor* × *C. bellatulum* has produced *C. × Godefroyæ*. These facts, therefore, suggest the idea that *C. niveum* is but a geographical—probably an island—form of *C. concolor*.

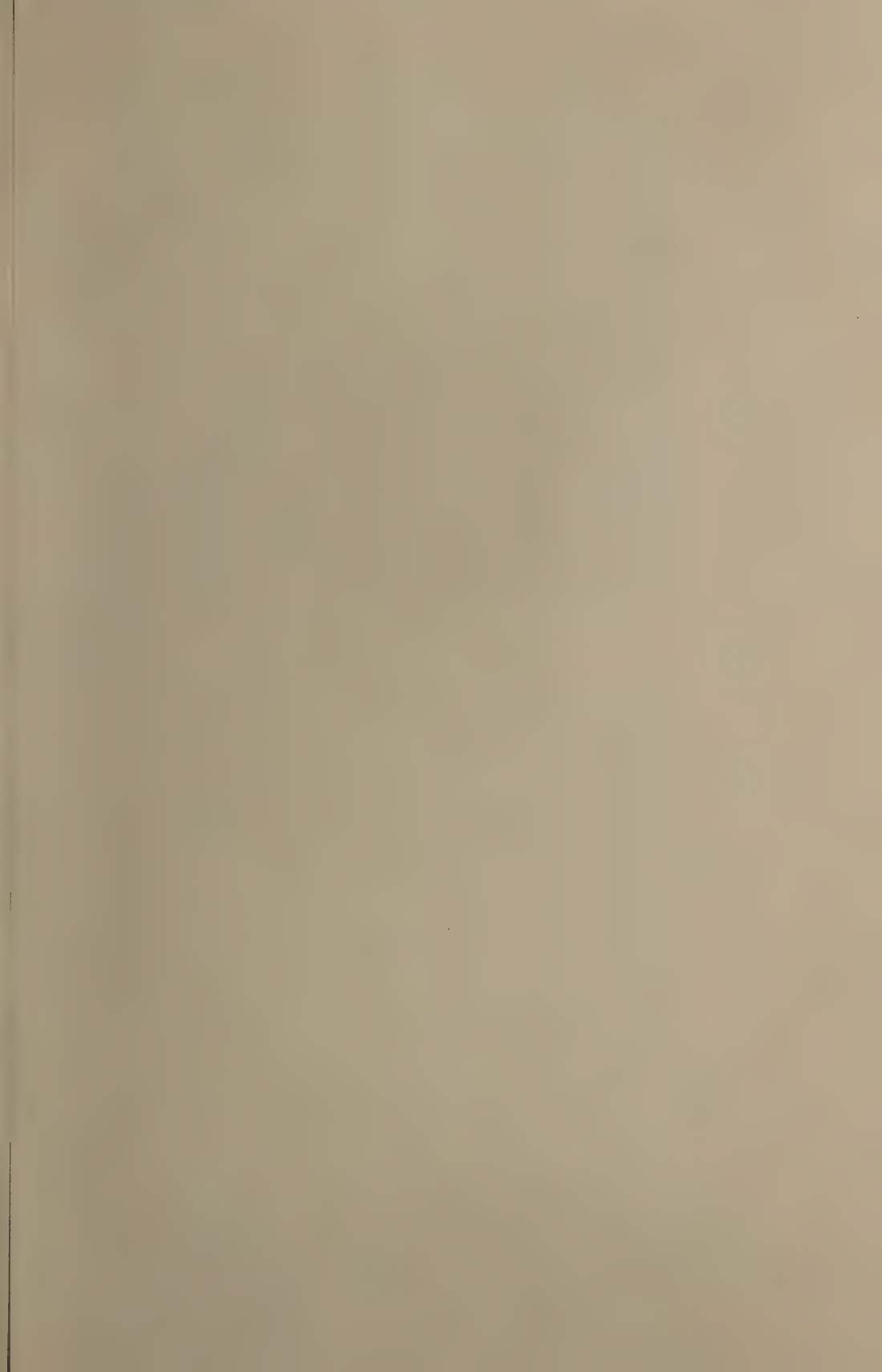
Viewed in this light Mr Grey's curious record may not be as impossible as it seems. *C. × Godefroyæ* = (*C. concolor* + *C. bellatulum*). Therefore *C. × Godefroyæ* ♀ × *C. niveum* ♂ would represent (*C. concolor* + *C. bellatulum*) ♀ × *C. niveum* ♂.

We have seen that *C. niveum* and *C. concolor* are very closely allied, and we know from experience how extremely variable all hybrids are after the first generation, and how common reversion becomes, so that

¹ According to the rules of priority this hybrid should be classed as a variety of *C. × Psyche*. Cf. Rolfe and Hurst in *The Orchid Stud-Book*, 1909, p. 196. (*Note added* 1914.)



Fig. 31. *Cypripedium niveum* Rehb. f.
(*Orchid Review*.)



it may not be so impossible, after all, to raise *C. concolor*, *C. niveum*, *C. × Godefroyæ*, *C. × G. leucochilum*, *C. × G. pure-white*, *C. bellatulum*, and nearly fifty intermediate forms from *C. × Godefroyæ* ♀ × *C. niveum* ♂.

It would be very interesting if someone would repeat the above cross and carefully record the result¹.

As with hybrids between species, so it is with crosses between varieties of the same species. For instance, Mr Norman Cookson crossed *Dendrobium nobile nobilius* ♀ with pollen of *D. n. Cooksoni*, and from the same seed-pod flowered "some good forms of each parent variety (*i.e.* *D. n. nobilius* and *D. n. Cooksoni*), and a series of forms grading down to ordinary *D. nobile*." (*Orch. Rev.* III. p. 168.) "In the progeny, all of which bear very fine flowers, no two are alike: a few are

¹ The appearance in 1898, in the St John's Wood collection, of a fifth hybrid from *C. concolor* and *C. bellatulum* named *C. concolor-bellatulum* Walkerianum (fig. 35), which differs considerably from the four earlier hybrids that were identified with *C. Godefroyæ*, again raises the question of the origin and status of *C. Godefroyæ* and its various forms. A careful review of the known facts and the material available leads me to the conclusion that the various forms of *C. Godefroyæ* are most probably natural hybrids between the three species *C. bellatulum*, *C. concolor* and *C. niveum* which overlap around the Gulf of Siam, the forms with a yellow ground-colour being probably derived from *C. concolor*, and those with a white ground-colour from *C. niveum*.

The larger and more densely spotted forms which approach towards *C. bellatulum*, *e.g.* *C. G. leucochilum* (fig. 30) and *C. G. Hodgkinsonii* (fig. 29), seem to me to represent distinctly a secondary cross with *C. bellatulum*. The interesting fact that *C. G. leucochilum* (unlike *C. Godefroyæ*) is imported in large numbers, true to type like an ordinary species with its own minor variations (see fig. 36), suggests that here probably we have a definite case of a secondary natural hybrid establishing itself and behaving in all respects like a systematic species.

If this interpretation is correct, the case of *C. G. leucochilum* provides a striking illustration of the theory of the evolution of species by hybridisation noted by the writer in 1898 in *Nature* (see later, III.) and more recently developed on Mendelian lines in a masterly manner by Dr Lotsy of Haarlem in a communication to the Linnean Society of London in 1914, entitled "On the Origin of Species by Crossing." In the case of *C. Godefroyæ* a Mendelian analysis of the various forms should settle the question definitely. Unfortunately this section of the genus does not thrive at Burbage and I venture to appeal to those orchid growers who are successful in the culture of these plants to take the matter up in the interests of science and horticulture. The first step would be to try to self the more distinct forms of the wild *C. Godefroyæ*, especially the larger ones such as *C. G. leucochilum*, *C. G. xanthochilum* and *C. G. Hodgkinsonii*, and carefully compare their progeny. If however these forms prove to be self-sterile—as most *Cypripedium* hybrids seem to be at Burbage—the next step would be to try to cross the various forms *inter se* and also with the three original species, especially *C. bellatulum*, taking care to use, if possible, pure forms of the species imported from remote districts where they do not overlap. (*Note added 1914.*)

almost identical with *D. n. Cooksoni*,...a few are richly coloured like *D. n. nobilius*, one is a fine white near to *D. n. Schröderianum*, and all the forms and all the shades of colour are represented." (*Gard. Chron.* March 28, 1896, p. 391.)

We know from importations recently made by Messrs Sander & Co. ("Lang Tang" vars.) that all these varieties of *D. nobile* grow together in their native home, and therefore it is reasonable to suppose that they frequently intercross, making their history a very mixed one. We cannot, therefore, be surprised at the result of Mr Cookson's experiment: their history being so varied, their offspring tend to be as variable, *the mixing by crossing and the unmixing by many nuclear divisions causing true reversions to occur from time to time*¹.

Many curiosities of Orchid breeding have come to light during the past few years, but they are getting so numerous now that familiarity with them has bred indifference if not contempt. For instance, the raising of *Odontoglossum* seedlings used to be considered a rare curiosity, but recently more than half-a-dozen have flowered, and we hear of numbers of seedlings fast growing to maturity. Perhaps the most remarkable feature of the flowering of *Odontoglossum* hybrids raised by hand is the direct proof that they afford of the parentage of certain natural hybrids; and Mr R. A. Rolfe, of Kew, has been making a special study of this interesting question with valuable results. Thus *O. crispum* ♀ × *O. luteopurpureum* raised by M. Leroy for Baron Rothschild, of Paris, has proved the parentage of *O. × Wilckeanum*; Messrs Veitch's *O. nobile* ♀ × *O. triumphans* proved the parentage of *O. × excellens*; and Messrs Linden's *O. × cirrhosum* ♀ × *O. Hallii* that of *O. × elegans*. While, on the other hand, we have the beautiful *O. × crispo-Hallii* raised by Mr Cookson which cannot occur in a wild state, one parent growing in Colombia and the other in Ecuador.

The chief difficulty hitherto found in raising *Odontoglossums* has been the rearing of the seedlings. I myself have had thousands of good seeds which germinated but gradually died off.

STERILITY.

In other difficult subjects the trouble is to get pods to set at all; thus Mr Cookson tells us that he has never been able to get a pod of good seed on *Dendrobium Bensoniæ*. (*Gard. Chron.* February 27, 1897, p. 134.) Many *Dendrobium* species seem difficult to fertilise, especially the evergreen section of the genus.

¹ This statement is curiously near the idea of Mendelian segregation discovered some three years later. (*Note added 1914.*)



Fig. 36. × *Cypripedium Godefroyæ* var. *leucochilum* Measures ex Rolfe.

Showing 13 imported plants flowering in the Cambridge Lodge Collection
Natural hybrids from South Siam.

(Orchid Review.)

In 1892 Mr W. H. White, for the President of the Royal Horticultural Society, Sir Trevor Lawrence, Bart., of Burford, pollinated over 100 flowers of *D. fimbriatum*, but not a single seed-pod was obtained. (*Orch. Rev.* i. p. 17.) Mr F. Moore, of the Royal Infirmary, Liverpool, informs me that he has managed to set pods on the following *Dendrobiums* this year:—*D. aureum* ♀ × *D. crepidatum roseum* ♂, *D. nobile* ♀ × *D. Devonianum* ♂, *D. primulinum* ♀ × *D. fimbriatum oculatum* ♂, and *D. clavatum* ♀ × *D. crepidatum roseum* ♂ (in litt., Aug. 24, 1897).

The species of the nigro-hirsute section of *Dendrobium* are well known to be bad setters. Mr R. Eichel, of Bradford, tells me that for eight years he has failed to cross *D. formosum* with pollen of the deciduous section, but he has now seedlings two-and-a-half months old of *D. formosum* ♀ × *D. nobile* from four seed-pods (in litt., Aug. 15, 1897). This instance illustrates once more how misleading and unsatisfactory purely negative results are, and in this there is much hope for the future. However many times a cross has failed to set, we can never be sure that it may not be accomplished by someone. Very trifling conditions seem to affect the delicate and susceptible organs of reproduction, causing apparent sterility. For instance, it is said that *Epidendrum ciliare* can only be fertilised with success in the evening, when the flowers begin to emit their fragrant perfume. (*Orch. Rev.* v. p. 115.) (Mr Harry Veitch tells me that this is not so with him.) Again, Mr Eichel has found *E. vitellinum* very difficult to set seed, and still more difficult to raise plants; but Messrs Veitch and Sons have flowered *E. radico-vitellinum*, and have a number of pods maturing at Langley¹. On the other hand Messrs Veitch have failed to set a pod on *E. radicans*, whereas Mr Eichel tells me that he has plants up of *E. radicans* ♀ crossed with pollen of *E. Wallisii* and *Cattleya Bowringiana*; and Messrs Sander have also plants up of *E. radicans* ♀ × *E. Wallisii*. (*Orch. Rev.* v. p. 301.)²

Darwin cites some very remarkable curiosities in sterility, showing what slight causes affect the reproductive organs in the genus *Oncidium*. (*Animals and Plants*, II. pp. 114—116.) He shows from the observations and experiments of Dr Fritz Müller in Brazil that at least nine species

¹ Further evidence of failures with *E. vitellinum* as a female parent appears in *Orch. Rev.* XIV. (1906), p. 318 on the authority of Herr Paul Wolter of Magdeburg. (Note added 1914.)

² Since the above was written *E. radicans* ♀ has produced *E. Boundii* (*Orch. Rev.* XI. (1903), p. 175) and *Epidiacrium gattonense* (Rolfe and Hurst in *The Orchid Stud-Book*, 1909, p. 268), both in the collection of Sir Jeremiah Colman at Gatton Park. (Note added 1914.)

of *Oncidium*, including the well-known *O. flexuosum*, are perfectly self-sterile: they will not set seed if pollinated with pollen from the same plant, and yet they are perfectly fertile both in their pollen and their ovules when crossed with a distinct species, or, most curious of all, if pollinated with pollen of the same species but from a distinct individual plant. For instance, on the stigma of *O. flexuosum* Dr Müller put the plant's own pollen side by side with pollen of another plant of the same species; in five days the latter was quite fresh and yellow, while the former was dark brown and decayed. Again, he placed on another stigma of *O. flexuosum* pollen of a distinct plant of the same species side by side with pollen from a distinct genus, *Epidendrum*: both behaved alike, and after eleven days could not be distinguished except by their caudicles. Dr Müller also found that the self-sterile pollen not only turned brown and decayed itself, but that it also caused the surface of the stigma to decay.

A few experiments carried out at Burbage confirm those made by Dr Müller in Brazil. Seventy-three flowers of *O. flexuosum* were pollinated with their own pollen: the stigma-chamber folded itself up in every case and swelled slightly, but in a few days withered from the stalk upwards and dropped off. Exactly the same result was obtained with *O. incurvum*, after pollinating many flowers. In all cases the pollen decayed quickly. It was different with *O. flexuosum* crossed with *O. Forbesii*: six flowers only were pollinated and two of them set pods, one of which burst prematurely and was full of chaffy seeds, while the other opened properly 133 days after pollination, and on examination was found to contain a few good plump seeds, which under the microscope appeared to be healthy living germs full of green colouring matter. The seeds were very small and round, hollowed out on one side, not unlike a shell: they were duly sown on April 12, 1897, but as yet show no signs of germination. I have also set three apparently good pods of *O. incurvum* crossed with *O. flexuosum*, which have not yet ripened¹.

Hand-raised hybrids of *Oncidium* do not seem to have been flowered yet in this country, but I hope that in the near future attempts to raise them will prove more successful².

¹ The seeds obtained from these two crosses duly swelled and germinated but no plants were reared, owing probably to unfavourable cultural conditions. (*Note added 1914.*)

² The first garden hybrid in the genus *Oncidium* flowered with Messrs Charlesworth in 1909, about twelve years after the above was written. It was described in *Orch. Rev.* XVIII. (1910), p. 8 under the name of *O. hybridum* and was raised

THE INFLUENCE OF FOREIGN POLLEN ON THE RIPENING
OF SEED-PODS.

In the *Orchid Review*, IV. p. 41, Mr T. L. Mead, of Oviedo, Florida, U.S.A., writes:—"I note a great difference in the time required to ripen seed-pods, according to the species of pollen made use of: it seems to tend to a mean between the normal ripening time of the two parents." The writer gives several curious and interesting facts in support of his opinion, and in three cases at least there appears to be some ground for the theory. On the other hand, Mr Cookson writes (*Orch. Rev.* IV. p. 112):—"From careful observation I am strongly of opinion that the period necessary to produce fertile seed depends on the period usual with the mother parent, and that the male parent has little to do with it." In *Orch. Rev.* IV. p. 326, Mr Mead gives some exceptions to his former theory, and suggests that the influence of the foreign pollen may be individual rather than general. For instance, "*Lælia anceps* pollen seems invariably to cut down time needed to ripen pods of *Cattleya labiata* group by about six months; while the pollen of *C. labiata* does not appreciably lengthen the time needed by *L. anceps* pods to ripen.... *Broughtonia sanguinea*, which both with its own and with foreign pollen ripens its seeds in one-and-a-half to two months, has power to quicken the ripening of *C. Bowringiana*, with which it gave good seed in eight-and-a-half months."

It seems to me that in the foregoing instances one of the main factors in the period of ripening seed-pods has been overlooked, and that is the conditions under which these experiments were carried out. For instance, to take the case of *L. anceps*. On January 22, 1896, I pollinated *L. a. Sanderiana* with its own pollen; the seed-pod ripened good seed by June 15, 1896, or 145 days. On January 27, 1897, I crossed the same plant again with its own pollen, and it did not ripen its seed-pod until July 14, 1897, taking 169 days, showing a difference in period of ripening (for the same plant pollinated by same plant) of twenty-four days in two different years. This seems to show that, apart from foreign pollen, there are other disturbing factors which must be taken into account when considering the causes of lengthening and shortening period of ripening of seed-pods in Orchids.

from *O. tigrinum* × *O. lamelligerum*. A second plant of this hybrid flowered with Messrs Charlesworth in 1912 (*Orch. Rev.* XXI. (1913), p. 18). These seem to be the only two recorded in the genus up to the present date, though several generic hybrids appeared in 1913 from *Oncidium* × *Cochlioda* and *Oncidium* × *Odontoglossum*. (Note added 1914.)

Mr Reginald Young, of Sefton Park, Liverpool, has very kindly placed at my disposal a copy of his interesting stud-book, containing a complete list of his crosses in the Paphiopedium group of Cypripediums from 1892 up to August 31, 1897. On referring to this I find that *Cypripedium barbatum* has been used twenty-two times as a seed parent, and has been crossed nearly the year round from December to September. In these twenty-two instances there was an extreme difference between the longest and shortest period of ripening (from pollination onwards) of 149 days, or about five months, the longest time being 315 days, or ten-and-a-half months, and the shortest period 166 days, or five-and-a-half months; so that the difference between the longest and the shortest was nearly as much as the whole time of the shortest period. A further examination of the facts and figures points to the conclusion that one of the chief causes of the extreme difference lies in the season of the year the cross was made, for the pod which ripened quickest was pollinated on June 24; while that which ripened slowest was pollinated on December 8; and between December and June, with a few exceptions, there was a gradual shortening of the period of ripening, and from June to December a marked lengthening of that period. The average period of ripening for each month was as follows:—

December, 315 days; March, 234 days; April, 209 days; May, 216 days; June, 187 days; August, 210 days; September, 287 days. Thus it seems that on the average the nearer to Midsummer the flower was pollinated the quicker the pod ripened, and the nearer to Christmas the slower the pod ripened; and I think that there can be little doubt that this was due to the influence of the sun at those different periods. Further it may be noted that the pod which ripened slowest was formed and matured between December 8 and October 19 of the following year; while the pod which ripened quickest was formed and matured between June 24 and December 7 of the same year. This seems to suggest that the power of the sun is more quickening in the early stages of formation than at any other time. We have already seen from Dr Hildebrandt's observations that in *Cypripediums* some four months elapse between pollination and actual fertilisation, so that we may reasonably conclude that the growth of the pollen tubes, and the consequent fertilisation of the ovules, is considerably hastened by the power of the sun; and I hope our Italian friends will make use of the golden opportunities of sunny Italy.

It is evident from this that any experiments undertaken to test the influence of foreign pollen on the period of pod ripening must be carried

out under the same conditions of light and heat. On looking through Mr Young's records I found twenty plants that had been crossed, which fairly well corresponded with the above conditions. Each plant carried two pods which were both crossed at the same time, and thus each pair of pods would be under fairly equal conditions all round. I have tabulated the results as follows:—

Each Pair crossed with the same Species or Hybrid

Seed Parent	Pollen Parent	Pollinated	Pod Ripened
<i>C. javanicum</i>	<i>C. × Godefroyæ</i>	Aug. 9, 1893	May 29, 1894
	<i>C. × Godefroyæ</i>	Aug. 9, 1893	May 29, 1894
<i>C. barbatum</i>	<i>C. niveum</i>	June 4, 1894	Dec. 24, 1894
	<i>C. niveum</i>	June 4, 1894	Dec. 24, 1894
<i>C. × superciliare</i>	<i>C. bellatulum</i>	June 15, 1894	Jan. 29, 1895
	<i>C. bellatulum</i>	June 15, 1894	Jan. 29, 1895
<i>C. × ænanthum</i>	<i>C. bellatulum</i>	July 23, 1894	Feb. 6, 1895
	<i>C. bellatulum</i>	July 23, 1894	Feb. 6, 1895
<i>C. × Ashburtoniæ</i>	<i>C. bellatulum</i>	July 23, 1894	April 15, 1895
	<i>C. bellatulum</i>	July 23, 1894	April 15, 1895
<i>C. × calophyllum</i>	<i>C. bellatulum</i>	July 23, 1894	April 22, 1895
	<i>C. bellatulum</i>	July 23, 1894	April 22, 1895
<i>C. × Harrisianum</i>	<i>C. niveum</i>	Sept. 14, 1894	Aug. 13, 1895
	<i>C. niveum</i>	Sept. 14, 1894	Aug. 13, 1895
<i>C. × Harrisianum</i>	<i>C. Sanderianum</i>	Sept. 14, 1894	July 25, 1895
	<i>C. Sanderianum</i>	Sept. 14, 1894	Aug. 7, 1895 (13 days)
<i>C. barbatum</i>	<i>C. niveum</i>	May 29, 1895	Dec. 7, 1895
	<i>C. niveum</i>	May 29, 1895	Dec. 7, 1895
<i>C. venustum</i>	<i>C. × nitens</i>	Dec. 14, 1895	Dec. 2, 1896
	<i>C. × nitens</i>	Dec. 14, 1895	Dec. 2, 1896
<i>C. Appletonianum</i> <i>Poyntzianum</i>	<i>C. callosum</i>	Jan. 15, 1896	Dec. 16, 1896
	<i>C. callosum</i>	Jan. 15, 1896	Dec. 16, 1896
<i>C. Lawrenceanum</i>	<i>C. Mastersianum</i>	March 27, 1896	Nov. 18, 1896
	<i>C. Mastersianum</i>	March 27, 1896	Nov. 18, 1896
<i>C. bellatulum</i>	<i>C. × Harrisianum</i>	May 26, 1896	Dec. 3, 1896
	<i>C. × Harrisianum</i>	May 26, 1896	Dec. 3, 1896

In the above list we have thirteen plants, each bearing a pair of pods, each pollinated on the same day, and each pollinated by one

species or hybrid, the result being that every pair but one ripened on the same day; while in the exceptional pair there is a difference of thirteen days between the ripening of each pod, notwithstanding that the "pollen was taken from the same plant, same scape, and probably the same flower" (in litt., August 14, 1897).

Each Pair pollinated with two different Species or Hybrids.

Seed Parent	Pollen Parent	Pollinated	Pod Ripened	Difference
C. \times calophyllum	C. Chamberlainianum	Dec. 8, 1894	Oct. 31, 1895	0
	C. Spicerianum	Dec. 8, 1894	Oct. 31, 1895	
C. \times Leeatum	C. \times ceananthum	Jan. 1, 1895	Nov. 25, 1895	12 days
	C. Boxalli	Jan. 1, 1895	Dec. 7, 1895	
C. \times nitens	C. \times Canhamii	Dec. 14, 1895	Sept. 7, 1896	63 days
	C. \times ceananthum	Dec. 14, 1895	Nov. 9, 1896	
C. \times Williamsianum	C. \times Calypso	Jan. 15, 1896	Sept. 26, 1896	0
	C. Boxalli	Jan. 15, 1896	Sept. 26, 1896	
C. bellatulum	C. Curtisii	May 26, 1896	Mar. 17, 1897	22 days
	C. ciliolare	May 26, 1896	Feb. 23, 1897	
C. niveum	C. \times Rittellii	May 26, 1896	April 9, 1897	31 days
	C. barbatum	May 26, 1896	Mar. 9, 1897	

In the above list we have six plants, bearing each a pair of pods, each pair pollinated on the same day, but each pair with two different species of pollen. The results are very interesting. Four out of the six ripened differently in each pair, the period varying from twelve to sixty-three days: in the other two each pair ripened together. The most curious and puzzling result of all was a plant of *C. Lawrenceanum* which carried three pods: two crossed with *C. Sanderianum* and one with *C. niveum*, all on the same day. There was a difference of fifteen days in the two pods crossed with *C. Sanderianum*, though the pollen was taken from the "same plant, same scape, and same flower"; while, strangely enough, the pod crossed with *C. niveum* ripened on the same day as one of those crossed with *C. Sanderianum*¹.

Looking at these twenty instances as a whole, it seems quite possible that the pollen parent has some influence on the period of ripening of the seed-pod, though to what extent is not quite clear.

Further experiments and observations are necessary before we can venture to determine the question definitely.

¹ *C. Sanderianum* was also the pollen parent in the one exception on p. 15.



Fig. 37. × Læliocattleya Aphrodite Lee ex O'Brien.

A generic hybrid out of *Cattleya Mendelii* by *Laelia purpurata* (fig. 4). From a specimen in the Westonbirt collection.
(*Orchid World*.)

CROSSES BETWEEN DIFFERENT GENERA.

In 1887, Mr R. A. Rolfe, of Kew, read a valuable paper before the Linnean Society on "Bigeneric Orchid Hybrids" (*Journ. Linn. Soc.* xxiv. 160, p. 156). In this paper Mr Rolfe gave a complete list of generic hybrids which had flowered up to 1887, and their number was then fifteen all told. A decade has passed away since then, and the small band of fifteen has increased in number to 118; and of these thirty-seven are generic hybrids of the second generation, and one of these is a trigeneric hybrid¹.

I have prepared a list of generic hybrids made up to 1897, with a reference to each, and the name of the original raiser.

LIST OF GENERIC ORCHID HYBRIDS.

(a) FLOWERED HYBRIDS.

(1) *Cattleya* × *Lælia* (*Lælio-Cattleya* ×).

- L.-C. × *albanensis* (L. *grandis* ♀ × C. *Warneri*), *Lindenia* t. 466, Linden, 1895.
 L.-C. × *Amesiana* (L. *crispa* ♀ × C. *maxima*), *Gard. Chron.* 1884, i. p. 109, Veitch.
 L.-C. × *Aphrodite* (C. *Mendelii* ♀ × L. *purpurata*), R.H.S., June 11, 1895, Lee (fig. 37).
 L.-C. × *Ascania* (C. *Trianae* ♀ × L. *xanthina*), R.H.S., April 25, 1893, Veitch.
 L.-C. × *Astoriae* (C. *Gaskelliana* ♀ × L. *xanthina*), R.H.S., Feb. 13, 1894, Sander.
 L.-C. × *Aurora* (L. *Dayana* ♀ × C. *Loddigesii*), *Gard. Chron.* Oct. 5, 1889, Veitch.
 L.-C. × *belairensis* (C. *Bowringiana* ♀ × L. *autumnalis*), R.H.S., Oct. 27, 1896, Mantin.
 L.-C. × *bella* (L. *purpurata* ♀ × C. *labiata*), *Gard. Chron.* 1884, i. p. 174, Veitch.
 L.-C. × *Boylei* (C. *Trianae* ♀ × L. *anceps*), R.H.S., May 23, 1894, Sander.
 L.-C. × *Bryan* (C. *Gaskelliana* ♀ × L. *crispa*), R.H.S., Sept. 8, 1896, Cookson.
 L.-C. × *callistoglossa* (L. *purpurata* ♀ × C. *Warszewiczii*), *Gard. Chron.* 1882, i. p. 76, Veitch.
 L.-C. × *Canhamiana* (L. *purpurata* ♀ × C. *Mossiae*), *Gard. Chron.* 1885, ii. p. 6, Veitch.
 L.-C. × *Clive* (C. *Dowiana* ♀ × L. *pumila*), R.H.S., Aug. 29, 1893, Cookson.
 L.-C. × *Cornelia* (L. *pumila* ♀ × C. *labiata*), R.H.S., Nov. 28, 1893, Veitch.
²L.-C. × *Crispo-Warneri* (C. *Warneri* ♀ × L. *crispa*), R.H.S., Nov. 13, 1894, Cowper.
 L.-C. × *Decia* (L. *Perrinii* ♀ × C. *Dowiana*), R.H.S., Oct. 27, 1894, Veitch.
 L.-C. × *devoniensis* (L. *crispa* ♀ × C. *guttata*), R.H.S., Sept. 22, 1863, Veitch.
 L.-C. × *Doris* (L. *harpophylla* ♀ × C. *Trianae*), *Orch. Rev.* ii. p. 79, Cookson, 1894.

¹ At the time of the preparation of *The Orchid Stud-Book* at the end of 1907 the number of distinct generic crosses had increased to 517, of which 14 are trigenera. (Note added 1914.)

² Now named L.-C. *Cowperi*, Rolfe and Hurst, *Orchid Stud-Book*, 1909, p. 100. (Note added 1914.)

- L.-C. \times Electra (C. Percivaliana \varnothing \times L. purpurata), R.H.S., June 9, 1896, Ingram.
 L.-C. \times elsteadensis (C. bicolor \varnothing \times L. xanthina), R.H.S., Aug. 13, 1895, Ingram.
 L.-C. \times epicasta (L. pumila \varnothing \times C. Warscewiczii), R.H.S., Aug. 29, 1893, Veitch.
 L.-C. \times Eumæa (C. Trianæ \varnothing \times L. grandiflora), R.H.S., Oct. 24, 1893, Veitch.
 L.-C. \times Eunomia (L. Dayana \varnothing \times C. Gaskelliana), R.H.S., Sept. 10, 1895, Veitch.
 L.-C. \times eximia (C. Warneri \varnothing \times L. purpurata), R.H.S., June 24, 1890, Veitch.
 L.-C. \times exoniensis (C. Mossiæ \times L. crispa), *Gard. Chron.* 1867, p. 1144, Veitch.
 L.-C. \times Ghislainæ (L. harpophylla \varnothing \times C. amethystoglossa), *Orch. Rev.* iv. p. 39, Imschoot. 1896.
 L.-C. \times Hippolyta (L. cinnabarina \varnothing \times C. Mossiæ), R.H.S., March 29, 1890, Veitch.
 L.-C. \times highburiensis (C. Lawrenceana \varnothing \times L. cinnabarina), R.H.S., April 7, 1896, Chamberlain.
 L.-C. \times Honore L. Perrinii \varnothing \times C. Percivaliana), R.H.S., Nov. 10, 1896, Ingram.
 L.-C. \times Hyeana (L. purpurata \varnothing \times C. Lawrenceana), Soc. Roy. Flor. Brux. Terv., May 9, 1897, Hye.
 L.-C. \times Ingrami (L. Dayana \varnothing \times C. Dowiana), R.H.S., July 13, 1892, Ingram.
¹L.-C. \times Ingramiana (L. purpurata \varnothing \times C. Dowiana), R.H.S., April 7, 1896, Ingram.
²L.-C. \times intermedio-flava (C. intermedia \varnothing \times L. flava), *Orch. Hyb.* p. 265, Fournier. 1896.
 L.-C. \times Marriottiana (L. flava \varnothing \times C. Skinneri), R.H.S., April 12, 1892, Marriott.
 L.-C. \times Maynardi (L. Dayana \varnothing \times C. Walkeriana), R.H.S., Feb. 14, 1893, Sander.
 L.-C. \times Measuresii (L. xanthina \varnothing \times C. dolosa), R.H.S., July 24, 1897, Sander.
 L.-C. \times Meteor (L. Dayana \varnothing \times C. Bowringiana), R.H.S., Nov. 10, 1896, Ingram.
 L.-C. \times Minerva (L. Perrinii \varnothing \times C. Lawrenceana), R.H.S., Nov. 10, 1896, Ingram.
 L.-C. \times Mylamiana (C. granulosa \varnothing \times L. crispa), *Gard. Chron.* 1876, ii. p. 740.
 L.-C. \times Myra (C. Trianæ \varnothing \times L. flava), R.H.S., March 12, 1895, Veitch.
 L.-C. \times Nysa (L. crispa \varnothing \times C. Warscewiczii), R.H.S., Aug. 25, 1891, Veitch.
 L.-C. \times olivetensis (L. pumila \varnothing \times C. Leopoldi), Soc. Nat. Hort. France, July 22, 1897, Mantin.
 L.-C. \times Pallas (L. crispa \varnothing \times C. Dowiana), R.H.S., Dec. 10, 1889, Veitch.
 L.-C. \times Parysatis (C. Bowringiana \varnothing \times L. pumila), *Orch. Rev.* ii. p. 310, Veitch. 1893.
 L.-C. \times Pisandra (L. crispa \varnothing \times C. Eldorado), R.H.S., Oct. 24, 1893, Veitch.
 L.-C. \times Proserpine (L. Dayana \varnothing \times C. velutina), *Gard. Chron.* 1890, p. 352, Veitch.
 L.-C. \times Reginæ (L. purpurata \varnothing \times C. Forbesii), Soc. Nat. Hort. Fr., July 22, 1897, Mantin.
 L.-C. \times Roeblingii (L. purpurata \varnothing \times C. Gaskelliana), R.H.S., June 25, 1895, Sander.
 L.-C. \times Rothschildiæ (L. Perrinii \varnothing \times C. Warscewiczii), *Orch. Rev.* iii. p. 353, Veitch. 1895.
 L.-C. \times Sallieri (L. purpurata \varnothing \times C. Loddigesii), *Journ. des Orch.* vii. p. 290, Maron. 1895.
 L.-C. \times Schröderæ (C. Trianæ \varnothing \times L. Jongheana), R.H.S., Aug. 23, 1892, Schröder.
 L.-C. \times Semiramis (L. Perrinii \varnothing \times C. Gaskelliana), R.H.S., Nov. 12, 1895, Veitch.
 L.-C. \times Statteriana (L. Perrinii \varnothing \times C. labiata), *Gard. Chron.* Nov. 14, 1893, Veitch.
 L.-C. \times Timora (L. Dayana \varnothing \times C. Lueddemanniana), *Gard. Chron.* Oct. 8, 1887, Veitch.

¹ A synonym of L.-C. Dominiana Veitch, 1878. (Note added 1914.)

² Now named L.-C. Fournieri, Rolfe and Hurst, *Orchid Stud-Book*, 1909, p. 103. (Note added 1914.)



Fig. 38. \times *Sophrocattleya Calypso* Rolfe.

A generic hybrid out of *Sophranitis grandiflora* by *Cattleya Loddigesii* (fig. 43).
- (*Gardeners' Chronicle*.)



Fig. 39. Brassavola Digbyana Lindl.

A native of Honduras. ♂ parent of fig. 40.

(*Orchid Review.*)



L.-C. \times Tresederiana (C. Loddigesii \varnothing \times L. crispa), *Gard. Chron.* Feb. 4, 1888, Treseder.

L.-C. \times Tydea (L. pumila \varnothing \times C. Trianae), R.H.S., Feb. 13, 1894, Veitch.

¹ L.-C. \times Vedasti (L. pumila \varnothing \times C. Loddigesii), *L'Orchid.* Feb. 1896, Perrenoud.

L.-C. \times Veitchiana (C. labiata \varnothing \times L. crispa), *Gard. Chron.* 1874, i. p. 566, Veitch.

L.-C. \times Zephyra (C. Mendelii \varnothing \times L. xanthina), R.H.S., July 24, 1894, Veitch.

In addition to the above there are thirty-six Hybrid Lælio-Cattleyas of the second generation (*i.e.* Lælio-Cattleya \times Lælia and Lælio-Cattleya \times Cattleya). For references see Hansen's *Orchid Hybrids*, pp. 85, 249, 258.

(2) *Cattleya* \times *Sophronitis* (*Sophro-Cattleya* \times).

S.-C. \times Batemaniana (S. grandiflora \varnothing \times C. intermedia), *Gard. Chron.* Aug. 28, 1886, Veitch.

S.-C. \times Calypso (S. grandiflora \varnothing \times C. Loddigesii), *Gard. Chron.* Nov. 22, 1890, Veitch. (Fig. 38.)

S.-C. \times eximia (C. Bowringiana \varnothing \times S. grandiflora), R.H.S., Sept. 24, 1894, Veitch.

(3) *Cattleya* \times *Brassavola* (*Brasso-Cattleya* \times).

² B.-C. \times Digbyano-Mossiae (C. Mossiae \varnothing \times B. Digbyana), *Gard. Chron.* June 15, 1889, Veitch.

³ B.-C. \times Digbyano-Trianae (C. Trianae \varnothing \times B. Digbyana), R.H.S., April 3, 1897, Veitch. (Fig. 40.)

(4) *Cattleya* \times *Epidendrum* (*Epi-Cattleya* \times).

E.-C. \times matutina (C. Bowringiana \varnothing \times E. radicans), R.H.S., March 23, 1897, Veitch. (Fig. 44.)

(5) *Lælia* \times *Sophronitis* (*Sophro-Lælia* \times).

S.-L. \times læta (L. Dayana \varnothing \times S. grandiflora), R.H.S., Oct. 9, 1894, Veitch.

S.-L. \times Marriotti (S. grandiflora \varnothing \times L. flava), R.H.S., Nov. 24, 1896, Marriott.

(6) *Lælia* \times *Epidendrum* (*Epi-Lælia* \times).

E.-L. \times belairensis (L. autumnalis \varnothing \times E. ciliare), *Cogn. Chron. Orch.* 1897, p. 53, Mantin.

E.-L. \times Hardyana (E. ciliare \varnothing \times L. anceps), R.H.S., Nov. 13, 1894, Rothschild. (Fig. 47.)

⁴ E.-L. \times radico-purpurata (L. purpurata \varnothing \times E. radicans), R.H.S., July 27, 1897, Veitch. (Fig. 45.)

(7) *Sophronitis* \times *Epidendrum* (*Epiphronitis* \times).

E.-ph. \times Veitchii (S. grandiflora \varnothing \times E. radicans), R.H.S., June 24, 1890, Veitch.

¹ Now named L.-C. Leeana, Rolfe, *Orch. Rev.* ix. (1901), p. 311. (*Note added 1914.*)

² Now named B.-C. Veitchii, Rolfe, *Orch. Rev.* x. (1902), p. 83. (*Note added 1914.*)

³ Now named B.-C. Sedeni, Rolfe, *Orch. Rev.* x. (1902), p. 84. (*Note added 1914.*)

⁴ Now named E.-L. Veitchii, Rolfe and Hurst, *Orch. Stud-Book*, 1909, p. 88, fig. 29. (*Note added 1914.*)

(8) *Phaius* × *Calanthe* (*Phaio-Calanthe* ×).

- P.-C. × *Berryana* (P. *Humblotii* ♀ × C. *Masuca*), R.H.S., Nov. 26, 1895, Sander.
 P.-C. × *Brandtiae* (P. *Wallichii* ♀ × C. × *Veitchii*), R.H.S., Feb. 9, 1897, Sander.
 P.-C. × *inspirata* (P. *grandifolius* ♀ × C. *Masuca*), *Man. Orch.* 1894, p. 146, Veitch.
 P.-C. × *irrorata* (P. *grandifolius* ♀ × C. *vestita*), *Gard. Chron.* 1867, p. 264, Veitch.
 P.-C. × *Sedeniana* (P. *grandifolius* ♀ × C. × *Veitchii*), *Gard. Chron.* Feb. 5, 1887, Veitch.

(9) *Zygopetalum* × *Colax* (*Zygo-Colax* ×).

- Z.-C. × *leopardinus* (Z. *maxillare* ♀ × C. *jugosus*), *Gard. Chron.* 1886, p. 199, Veitch.
 Z.-C. × *Veitchii* (Z. *crinitum* ♀ × C. *jugosus*), *Gard. Chron.* I. p. 765, 1887, Veitch.

(10) *Anæctochilus* × *Hæmaria* (*Anæctomaria* ×).

- A. × *Dominri* (A. *Roxburghii* × H. *discolor*), *Proc. R.H.S.* v. 1865, p. 139, Veitch.

(11) *Hæmaria* × *Macodes* (*Macomaria* ×).

- M. × *Veitchii* (H. *discolor* ♀ × M. *Petola*), *Proc. R.H.S.* II. 1862, p. 546, Veitch.

(12) *Hæmaria* × *Dossinia* (*Dossinimaria* ×).

- D. × *Dominri* (H. *discolor* ♀ × D. *marmorata*), *Gard. Chron.* 1861, p. 531, Veitch.

(13) *Sophronitis* × *Laelio-Cattleya* × (*Sopfro-Laelio-Cattleya* ×)¹.

- S.-L.-C. × *Veitchii* (S. *grandiflora* ♀ × L.-C. × *elegans*), R.H.S., Sept. 6, 1892, Veitch.

(b) GENERIC CROSSES FLOWERED MOTHER GENUS.

(1) *Zygopetalum* × *Odontoglossum*.

- Z. *Mackayi* ♀ × O. *bictonense*, Seden for Veitch (in litt., Sept. 25, 1897).
 Z. *Mackayi* ♀ × O. *crispum*, Seden for Veitch (in litt., Sept. 25, 1897).
 Z. *Mackayi* ♀ × O. *grande*, Seden for Veitch (in litt., Sept. 25, 1897).
 Z. *Mackayi* ♀ × O. *nobile* (*Pescatorei*), Seden for Veitch (in litt., Sept. 25), 1897;
 Treseder for Heath (in litt., Sept. 4, 1897).

(2) *Zygopetalum* × *Oncidium*.

- Z. *Mackayi* ♀ × O. *unguiculatum*, Eichel (in litt., June, 1897) (cf. Horner, in litt., Sept. 9, 1897).

(3) *Zygopetalum* × *Lycaste*.

- Z. *Mackayi* ♀ × L. *Skinneri*, Seden for Veitch (in litt., Sept. 25, 1897).
 (All the above flowered *Zygopetalum Mackayi* pure and simple.)

(4) *Phragmipedium* × *Paphiopedium*.

(South American × East Indian *Cypripedium*.)

- Phrag. *longifolium* ♀ × Paph. *Stonei*, Grey in *Orch. Hyb.* p. 189.
 (Flowered Phrag. *longifolium*.)

¹ Now named *Sophocatlaelia*, Rolfe, *Orch. Rev.* VIII. (1900), p. 354. (Note added 1914.)

(c) UNFLOWERED HYBRIDS.

- Bletia* × *Lælia* (B. verecunda ♀ × L. purpurata), Mead, *Orch. Rev.* iv. p. 42.
Bletia × *Schomburgia* (B. verecunda ♀ × S. tibicinis), Mead, *Orch. Rev.* iv. p. 42.
Bletia × *Phaius* (B. catenulata ♀ × P. grandifolius), Hodgkinson, *Orch. Rev.* iv. p. 334.
Bletia × *Cologyne* (B. hyacintha ♀ × C. cristata), Eichel, *Orch. Rev.* v. p. 140 (Moore, in litt., Aug. 31, 1897).
Epidendrum × *Phaius* (E. atropurpureum ♀ × P. grandifolius), Berkeley, *Orch. Hyb.* p. 322.
Epidendrum × *Zygopetalum* (Z. Mackayi ♀ × E. ciliare), Horner in *Garden*, Nov. 2, 1892.
Epidendrum × *Dendrobium* (E. × O'Brienianum ♀ × D. crystallinum), *Orch. Rev.* ii. p. 292, Statter.
Cattleya × *Sobralia* (S. macrantha ♀ × C. Warscewiczii), Chamberlain, *Orch. Rev.* i. p. 366.
Sophronitis × *Brassavola* (S. grandifolia ♀ × B. glauca) (Orpet, in litt., Sept. 1897).
Maxillaria × *Lycaste* (M. Sanderiana ♀ × L. Skinneri) (Eichel, in litt., Sept. 1897).
Diacrium × *Epidendrum* (D. bicornutum ♀ × E. radicans), Sander, *Orch. Rev.* v. p. 301.
Cattleya × *Phragmipedium* (Charlesworth, in litt., Oct. 1897).
Lælia × *Phragmipedium* (L. cinnabarina ♀ × P. × Sedeni) (Eichel, in litt., Sept. 1897 [3 lots]).
Paphiopedium × *Cypripedium* (E. Indian × Hardy *Cypripedium*) (P. Lawrenceanum ♀ × C. spectabile), Fröbel, *Gard. Chron.* Oct. 2, 1897.

Paphiopedium × *Phragmipedium*.(E. Indian × S. American *Cypripedium*.)

- Paph. Curtisi ♀ × Phrag. longifolium, Marwood, *Gard. Chron.* July 8, 1893.
Phrag. caudatum ♀ × Paph. barbatum, Veitch, R.H.S., May 12, 1885.
Paph. callosum ♀ × Phrag. caudatum, Lutwyche, *Orch. Rev.* ii. p. 19.
Paph. Parishii ♀ × Phrag. caricinum, Swan, *Orch. Rev.* ii. p. 171.
Phrag. × Sedeni ♀ × Paph. Stonei [(1) Statter, in litt., Aug. 1897]; (2) Hurst, 1897¹.
Paph. Spicerianum ♀ × Phrag. Schlimii, Hurst, 1897¹.
Paph. Spicerianum ♀ × Phrag. × Sedeni, Treseder, *Orch. Hyb.* p. 188.
Phrag. × Dominicanum ♀ × Paph. Chamberlainianum, Swinburne, *Gard. Chron.* Oct. 1896, p. 435.
Paph. × Ashburtoniæ ♀ × Phrag. × calurum, Winn, 1896.
Paph. venustum ♀ × Phrag. Schlimii, Winn, 1896.
Paph. bellatulum ♀ × Phrag. × Sedenii, Winn, 1896.
Phrag. × cardinale ♀ × Paph. Spicerianum, Hurst, 1897¹.

¹ These plants were not raised at Burbage, but were purchased at the sale of the Winn collection. Only five survived to flower and all flowered true to the mother species with no trace of the pollen "parent." As in the case of the *Zygopetalum* "false hybrids," noted later, varietal variation was distinctly evident. (*Note added* 1914.)

(d) GOOD SEEDS.

Cattleya × *Broughtonia* (*C. Bowringiana* ♀ × *B. sanguinea*), Mead, *Orch. Rev.* iv. p. 326.

Epidendrum × *Odontoglossum* (*E. vitellinum* ♀ × *O. crispum*), Eichel, *Orch. Rev.* v. p. 114.

Bletia × *Calanthe* (*B. hyacintha* ♀ × *C. Masuca*), Veitch, *Orch. Conf.* 1885.

Acanthophippium × *Chysis* (*A. Curtisi* ♀ × *C. bractescens*), Veitch, *Orch. Conf.* R.H.S., 1885, p. 35.

Chysis × *Mormodes* (*C. aurea* ♀ × *M. Pardinum*) (Moore, in litt., August, 1897).

Chysis × *Zygopetalum* (*C. aurea* ♀ × *Z. Sedeni*), Veitch, *Orch. Conf.* 1885.

Lælia × *Paphiopedium* (*L. cinnabarina* ♀ × *Paph. Boxalli*) (Eichel, in litt., Sept. 1897).

Paphiopedium × *Cypripedium* (*E. Indian* × *Hardy Cypripedium*), (*P. Exul* ♀ × *C. Calceolus*), Hurst, *Orch. Rev.* v. p. 365.

Cypripedium × *Phragmipedium* (*Hardy* × *S. American Cypripedium*), (*C. Calceolus* ♀ × *Phrag. Sedeni*), Hurst, *Orch. Rev.* v. p. 365.

CURIOUS GENERIC HYBRIDS.

(1) *Sophronitis* × *Epidendrum*.—*Epiphronitis* × *Veitchii* is an interesting hybrid out of *Sophronitis grandiflora* by *Epidendrum radicans* (fig. 46). It was first raised and flowered by Mr Seden for Messrs Jas. Veitch and Sons in 1890. The parents of this hybrid not only belong to distinct genera, but are markedly different both in size and habit, the male parent growing as many feet high as the female parent grows in inches; the former is a native of Mexico and Guatemala, and the latter of Southern Brazil. The hybrid is more curious still, the influence of the *Epidendrum* parent being overwhelming; the reed-like stems, with air-roots, show no trace of the *Sophronitis* parent, being exactly like *Epidendrum*¹, and in the flower there is hardly a trace of the peculiar structure of *Sophronitis*; but, on the other hand, one can see at a glance that some modifying influence has been at work: the flowers are darker in colour, the petals are broader, the lip is less toothed, broader, and not so deeply cleft, the crest has more yellow colour, two smaller tubercles, and a shorter keel—all of which are consistent with the influence of *Sophronitis*. But anyone not knowing the parentage of the hybrid would call it a dwarfed large-flowered and highly coloured form of *Epidendrum radicans* (col. fig. *Revue Horticole*, October 16, 1896, p. 480).

(2) *Cattleya* × *Epidendrum*.—*Epi-Cattleya* × *matutina* (fig. 44) is a curious hybrid out of *Cattleya Bowringiana* by *Epidendrum radicans*. It was raised and flowered by Mr Seden for Messrs Jas. Veitch

¹ Except in the dwarfer habit of growth. (Note added 1914.)



Fig. 44. \times *Epicattleya matutina* Rolfe

A dominant generic hybrid out of the pseudo-bulbous *Cattleya Bowringiana* Veitch by the reed-like *Epidendrum radicans* (fig. 46).

(*Gardeners' Chronicle*.)

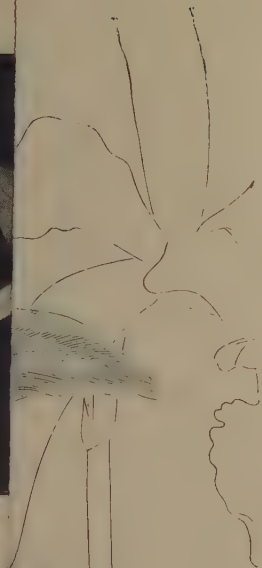


Fig.



Fig. ^TRECHRE

(chronicle).

trum ciliare L. by the

and Sons, and was shown in March 23, 1897. Like *Epiphronitis* × *Veitchii*, this hybrid closely resembles *Epidendrum radicans* both in habit and flowers, there being only a few traces of the mother parent *Cattleya Bowringiana*. But it is said that the reed-like stems show a slight tendency to thicken at the base; the colour of the sepals and petals, too, is much lighter than in *Epidendrum radicans*, being yellow tinged with vermilion; the lip is broader, ovate, and notched instead of three-lobed and toothed; otherwise the hybrid would easily pass for a large-flowered and light-coloured form of *Epidendrum radicans*.

(3) *Lælia* × *Epidendrum*.—*Epi-Lælia* × *radico-purpurata*¹ is a beautiful hybrid of the same class out of *Lælia purpurata* (fig. 4) by *Epidendrum radicans* (fig. 46), and like the other two was raised by Mr Seden for Messrs Jas. Veitch and Sons, and was shown at the R.H.S. on July 27, 1897. This hybrid again shows the predominating influence of the *Epidendrum* parent, though the *Lælia* parent is rather more perceptible than in either *Epiphronitis* × *Veitchii* or *Epi-Cattleya* × *matutina*. The reed-like habit and the adnate column are those of *Epidendrum*, while traces of the *Lælia* are to be seen in the slightly recurved leaves, larger flowers, sepals and petals modified in colour to a light flame yellow; the lip is broadly ovate and nearly entire with a broad band of purple around two lemon yellow eyes, with a three-keeled crest between. Thus in essential structure the hybrid corresponds with *Epidendrum radicans*, yet from a horticultural point of view it is far superior in every way.

In all three hybrids, between *Sophranitis* and *Epidendrum*, *Cattleya* and *Epidendrum*, and *Lælia* and *Epidendrum*, we find the *Epidendrum* parent so largely and overwhelmingly the predominant partner that did we not know we could never have guessed the other parent.

It will be noticed that the *Epidendrum* parent is the same species (*E. radicans*) in each of the three cases, and at first sight it might be thought that this species was, in some way or other, naturally prepotent over other species; but we know that this is not so, for when *E. radicans* is crossed with *E. xanthinum* the offspring *E. × dellense* is intermediate in character, slightly inclining to *E. xanthinum* (*Orch. Rev.* i. p. 324); and *E. radicans* crossed with *E. evectum* produces *E. × O'Brienianum*, the colour of which is intermediate, but the shape resembles *E. evectum* (*Orch. Rev.* i. p. 227). It is evident, therefore, that *E. radicans* is not always predominant when used as a parent.

The genus *Epidendrum* contains a large number of species, which fall naturally into at least two distinct groups.

¹ Now named *Epilælia Veitchii* (fig. 45). (Note added 1914.)

(1) Eu-epidendrum of Bentham and Hooker, *Genera Plantarum*, III. p. 529 (1883). (a) Column and lip wholly adnate; (b) Stems reed-like.

(2) Other groups of Bentham. (a) Column and lip partly adnate; (b) stems thickened or swollen into pseudo-bulbs.

It will be noted that these two groups are very distinct in structure, almost distinct enough to be classed as two genera; and further it is apparent that both in the freedom of column and lip and in the swollen stems the second group approaches *Lælia*, *Cattleya*, and *Sophronitis*, forming as it were a connecting link between them and the reed-like *Epidendra*. Indeed, recent results of hybridisation seem to show that the second group of *Epidendrum* is more closely allied to *Cattleya*, *Lælia*, and *Sophronitis* than to the first group. Thus *E. ciliare* of the second group when crossed with *Lælia anceps* and *L. autumnalis* produces ordinary hybrids fairly intermediate in character (*Epi-Lælia* × *Hardyana* (fig. 47) and *E.-L.* × *belairensis* respectively); whereas when *E. vitellinum* of the second group is crossed with *E. radicans* of the first group the result is similar to crossing *E. radicans* with *Sophronitis*, *Cattleya*, and *Lælia*—namely, a slightly modified *E. radicans* (the only traces of the mother parent *E. vitellinum* being a slightly glaucous tint of the leaves, a tendency of the reed-like stems to enlarge at the nodes, together with irregularly modified flowers, *E. × radico-vitellinum* O'Brien, *Gard. Chron.* July 10, 1897, p. 16)¹.

To sum up briefly we find that—

(1) *Cattleya*, *Lælia*, *Sophronitis*, and the pseudo-bulbous *Epidendra* when intercrossed produce normal hybrids intermediate in character.

(2) The reed-like *Epidendra* when united with one another also produce ordinary hybrids intermediate in character.

(3) But when the reed-like *Epidendra* are crossed with the pseudo-bulbous *Epidendra* or with *Cattleya*, *Lælia*, and *Sophronitis* abnormal hybrids are produced having the essential characters of the reed-like *Epidendra*.

And, having regard to recent researches into the nature of fertilisation, we are almost bound to conclude that *Cattleya*, *Lælia*, *Sophronitis*, and the pseudo-bulbous *Epidendra* contain in their germ-cells some nuclear particles of the reed-like *Epidendra*².

¹ Now named *E. Cassiope*, Rolfe and Hurst, *Orchid Stud-Book*, 1909, p. 86. (Note added 1914.)

² In the light of Mendelism this conclusion of 1897 based on the work of Weismann seems to be unnecessary, and the results can now be more simply interpreted



Fig. 49. × *Dialælia Veitchii* O'Brien.

A dominant generic hybrid from

Fig. 48. *Diacrium bicornutum* Benth. and Fig. 50. *Lælia cinnabarina* Lindl.

(*Orchid Review*.)



Fig. 51. \times *Diacattleya Colmaniae* Rolfe.

An intermediate generic hybrid out of *Diacrium bicornutum* (fig. 48) by *Cattleya intermedia* (fig. 56).
(*Orchid Review*.)

These remarkable curiosities in Orchid breeding therefore go far to prove that not only are the pseudo-bulbous *Epidendrum* (like *E. vitellinum*) descended from a reed-like *Epidendrum* ancestor, but that it is highly probable that *Sophranitis grandiflora*, *Laelia purpurata*, and *Cattleya Bowringiana* are also so descended¹.

This opens up a wide field for the student of evolution—a field into which we cannot enter now, being beyond the scope of these notes.

PREPOTENT GENERIC CROSSES.

Certain crosses between distinct genera have, curiously enough, flowered the same genus and species as their mother parent. The following is a complete list so far as I have been able to ascertain:

PHRAGMIPEDIUM × PAPHIOPEDIUM.

(South American *Cypripedium* × E. Indian *Cypripedium*.)

- (1) *Phrag. longifolium Hartwegii* ♀ × *Paph. Stonei* ♂.

Raised by Mr R. M. Grey for Mr Graves, Orange, Mass. "The plant resembled the seed-bearing parent very closely." (Hansen, *Orchid Hybrids*, p. 189.)

ZYGOPETALUM × ODONTOGLOSSUM.

- (1a) *Z. Mackayi* ♀ × *O. nobile (Pescatorei)* ♂.

"A few seedlings raised by Mr Seden for Messrs J. Veitch and Sons, all of which flowered pure *Z. Mackayi*." (In litt., September 25, 1897.)

(1b) The same cross was made by Mr Treseder for Messrs Heath and Son of Cheltenham. "About 300 seedlings were raised, and about twenty plants flowered pure *Z. Mackayi*." (In litt., September 4, 1897.)

- (2) *Z. Mackayi* ♀ × *O. crispum* ♂.

- (3) *Z. Mackayi* ♀ × *O. grande* ♂.

- (4) *Z. Mackayi* ♀ × *O. bicktonense* ♂.

as cases of Mendelian dominance. The factor for reed-like stems may be regarded as epistatic and the factor for pseudo-bulbous stems as hypostatic; the single presence of the factor for reed-like stems being sufficient to give a reed-like F_1 without presuming the existence of like factors in the pseudo-bulbous parent. Owing however to the complete sterility of these hybrids it has not yet been possible to demonstrate this experimentally. (Note added 1914.)

¹ A Mendelian interpretation of these results tends to confirm the suggestion of 1897 that the pseudo-bulbous species of *Epidendrum*, *Sophranitis*, *Laelia* and *Cattleya* may have descended from a reed-like ancestor. For, a loss of the epistatic factor for reed-like stems would result in the appearance of the hypostatic pseudo-bulbous stems. (Note added 1914.)

"A few seedlings of *each* cross" were raised by Mr Seden for Messrs Veitch and Sons. "All of which flowered pure *Z. Mackayi*." (In litt., September 25, 1897.)

ZYGOPETALUM \times ONCIDIUM.

(1 *a*) *Z. Mackayi* ♀ \times *O. unguiculatum* ♂. A plant raised in Florence, Italy, by a friend and correspondent of Mr Eichel, of Bradford, 'has flowered pure and simple *Z. Mackayi*.'

(1 *b*) Rev. F. D. Horner, of Burton-in-Lonsdale, Kirkby Lonsdale, tells me that he had three seedlings of this same cross, which he grew for four or five years, but they unfortunately died before flowering; "but the plants seemed the fac-simile of *Z. Mackayi* in both bulbs and foliage....All experts who saw them called them *Z. Mackayi* plants." (In litt., September 9, 1897.)

ZYGOPETALUM \times LYCASTE.

(1) *Zygopetalum Mackayi* ♀ \times *Lycaste Skinneri* ♂. "A few seedlings," raised by Mr Seden for Messrs Veitch and Sons, "which all flowered pure *Z. Mackayi*." (In litt., September 25, 1897.)

These curious generic crosses are particularly interesting, and are perhaps the strangest in the history of hybridisation. They are analogous to the three curious offspring of *Epidendrum radicans* mentioned above, being similar in some respects, but they are not parallel cases, because in other respects they differ much. In the offspring of *E. radicans* some traces of modification are apparent to the most casual observer, but in these there does not seem to be the faintest or slightest trace of the other parent. In the offspring of *E. radicans* the male parent was the predominant one, and therefore there could be no chance of accidental self-fertilisation or parthenogenesis, whereas in these we are now dealing with it is the female parent which is all powerful; and it is quite open for the sceptic to suggest that these curious results are due to self-fertilisation, or that they were produced without the aid of pollen. But, on the other hand, it is easy to show that self-fertilisation is out of the question in all these crosses, and that in the *Zygopetalum* crosses, at all events, parthenogenesis is equally out of court¹.

With regard to self-fertilisation:—(*a*) Mr Grey writes that in his *Phragmipedium* \times *Paphiopedium* "the pollen was removed from the seed-bearing plant before the flower was fully expanded." (*Orchid*

¹ Later results suggest that these cases may quite possibly be due to a peculiar kind of parthenogenesis. (*Note added 1914.*)

Hybrids, p. 189.) (b) *Zygopetalum* × *Odontoglossum* and *Lycaste*. Mr Seden writes: "I am quite sure the pollen was removed from the *Z. Mackayi* in every case." (c) *Zygopetalum* × *Oncidium*. Mr Eichel writes: "I have so much confidence...that the probability of self-fertilisation of the *Zygopetalum* flower is out of the question," and Rev. F. D. Horner writes: "I am confident of one thing, and that is that no pollen of the seed-parent (the *Zygopetalum*) had any part in the production of these seedlings." So that in all these cases it is manifest that self-fertilisation is a broken reed to lean upon for an explanation.

Perhaps I might here point out the difference between these cases and the *Cypripedium* curiosities mentioned before, which I have attributed to accidental self-fertilisation¹.

These nine cases are all that have been tried between these genera, so far as we know, and all have had the same result, being the rule and not the exception; whereas the *Cypripedium* cases were but a few curiosities out of hundreds of normal hybrids, and therefore the exception rather than the rule. With regard to the suggestion of parthenogenesis I cannot deny that Mr Grey's cross between *Phragmipedium* and *Paphiopedium* might possibly be due to this, especially as the plant closely resembled the mother parent variety as well as species, and only differed but slightly in size of flower. Parthenogenesis, or the production of fertile seeds in a pod without the aid of pollen, is well known to occur in certain plants (see Kerner and Oliver, *Natural History Plants*, II. p. 469; *Gardeners' Chronicle*, August 23, 1890, p. 218); and Prof. Henslow in his *Structure of Flowers*, p. 171, refers to an interesting discovery accidentally made by Dr Treub. Dr Treub found a larva of an insect in the ovary of a Mauritian Orchid, *Liparis latifolia*: it did not injure either the ovules or the ovary, but seemed to feed on the juices secreted by the ovarian cavity. In this cavity, *without the aid of pollen*, the ovules developed and became covered with seed-coats, as if under the influence of pollination, so that the irritation of the larva determined the development of the ovules in the same way that the pollen tubes would have done.

This possibly may have happened with Mr Grey's plant. The pollen tubes of *Paph. Stonei* may have irritated and developed the ovules by feeding on the juices of the pod, and in some way failed to fertilise the egg-cell, the result being a seed-bud developed within the pod bearing the characters of the mother species and the mother variety. But it is not fair or proper to generalise from an isolated instance like this; we

¹ Cf. 1914 footnote on p. 16.

must wait patiently for further results before we attempt to assign or determine the real cause of this curiosity.

But in the case of the *Zygopetalum* crosses we can make more sure of our ground. If these were caused by parthenogenesis all the plants would be alike from one pod¹; but this was not so, for Mr Seden writes to me that "all the seedlings varied, the same as all imported plants in size and colour," and we know that one of Mr Treseder's plants differed in colour from its birth-mates, "the lip being almost wholly white, with a few slight purple marks at base and centre, and the margin was more wavy in outline" (shown at Royal Horticultural Society's meeting, December 15, 1896).

Therefore it is manifest that neither self-fertilisation nor parthenogenesis will hold good in these cases². Nor can they be due to the natural prepotency of *Z. Mackayi* as a parent, for we know of three other hybrids at least, having *Z. Mackayi* as a parent, which are all fairly intermediate in character:—(1) *Z. × Sedeni* (*Z. maxillare* ♀ × *Z. Mackayi* ♂), Veitch, *Gardeners' Chronicle*, 1874, p. 290. (2) *Z. × leucochilum* (*Z. Mackayi* intermedium ♀ × *Z. Burkei* ♂), *Orchid Review*, iv. p. 62. (3) *Z. × Perrenoudi* (*Z. Mackayi* intermedium ♀ × *Z. Gauthieri* ♂), *Dict. Icon. Orch. Zygo. hyb.* pl. 1.

Nor can it be said that *Zygopetalum* as a genus is prepotent over other genera, for twice it has been crossed with *Colax*, and in both cases true hybrids, intermediate in character, have been raised.—(1) *Zygo-Colax × Veitchii*, Rolfe in *Linn. Soc. Jour.* xxiv. p. 170. (*Z. crinitum* ♀ × *C. jugosus* ♂.) (2) *Zygo-Colax × leopardinus* (*Z. maxillare* ♀ × *C. jugosus* ♂), Reich. *Gardeners' Chronicle*, 1886, i. p. 199.

So that, as far as our present knowledge goes, we can only account for the prepotency of *Zygopetalum* over *Odontoglossum*, *Oncidium*, and *Lycaste* in the same way that we have had to explain the predominance of *Epidendrum* over *Cattleya*, *Lælia*, and *Sophranitis*, namely, that in the germ-cells of *Odontoglossum*, *Oncidium*, and *Lycaste* there must be a certain proportion—a large proportion in these cases—of unmodified nuclear particles of *Zygopetalum*, and that, therefore, *Zygopetalum* is the common ancestor of *Odontoglossum*, *Oncidium*, and *Lycaste*, and that the three latter genera are more recent in their origin than the ancestral genus *Zygopetalum*. A somewhat interesting confirmation of this in regard to *Odontoglossum*, at any rate, is the fact that the

¹ Recent results suggest that segregation of characters may take place even in parthenogenesis. (Note added 1914.)

² Cf. 1914 footnote on p. 36.



Fig. 52. *Zygotetulum Mackayi* Hook var. *Fletcheri** Hurst (*Orchid Review*).

(Syn. *Chondropetalum Fletcheri* Rolfe, *Orch. Rev.* XVI. (1908), p. 56, f. 8.)

A "prepotent generic cross" raised by Messrs Sander & Sons at St Albans out of *Zygotetulum Mackayi* after pollination with *Chondrorhyncha Chestertonii* (fig. 53).

* Generically and specifically this plant is indistinguishable from *Zygotetulum Mackayi*, and also from the hundreds of other "false hybrids" raised out of *Z. Mackayi* after pollination with other genera. In several cases these "false hybrids" have been further tested gametically for at least two generations with the result that, so far, all behave as if they were *Z. Mackayi*, pure and simple. In these circumstances a new generic and specific name seems to be unnecessary. On the other hand, varietally these "false hybrids" differ considerably among themselves especially in the colour-markings of their flowers, and the figured form above may therefore be distinguished by the varietal name of *Fletcheri*, differing as it does from the type chiefly in the almost complete absence of the usual blue markings on the lip of the flower.

On the authority of Messrs Sander & Sons and their hybridist Mr Gott, Mr R. H. Compton states in *Orch. Rev.* XIX. (1911), p. 70, that the two varietal types *Z. Mackayi* and *Z. M. Fletcheri* appeared in this cross in about equal proportions.

This suggests that a definite segregation of factors, representing probably the presence and absence of blue markings on the lip, took place in the germ-cells, following the stimulation of pollination and previous to their parthenogenetic development into seeds. The further statement that an identical result was obtained from the reverse cross out of *Chondrorhyncha Chestertonii* after pollination with *Zygotetulum Mackayi* is difficult to follow, and it would be interesting to have the experiment repeated, as well as to have *Z. M. Fletcheri* crossed again with pollen of *C. Chestertonii*. (Note added 1914.)



Fig. 53. *Chondrorhyncha Chestertonii* Rehb. f.
Remarkable for its fringed petals and lip.
(*Orchid Review*.)

seedling *Odontoglossums* raised by M. Leroy for Baron Rothschild, of Paris, "during the first eighteen months of their growth resembled *Zygopetalum* more than they did *Odontoglossum*." (*Orchid Hybrids*, p. 226.) Students of embryology will appreciate this fact, for it is well known to them that all living beings tend to resemble their ancestors in the early stages of their development¹.

CURIOUS CROSSES.

In the *Orchid Review* for June 1897 I recorded a few curious generic crosses made by me during the early part of the year, with the results up to June 1. I venture to repeat them here with their progress up to date.

(1) *Lycaste Skinneri* ♀ × *Lælia anceps Sanderiana* ♂. Crossed February 15, 1897. A healthy-looking pod 5 inches in girth.

(2) *Lycaste Skinneri* ♀ × *Brassavola glauca* ♂. Crossed March 16, 1897. A good-looking pod 5 inches in girth.

(3) *Cypripedium Calceolus* ♀ × *Phragmipedium* × *Sedenii candidulum* ♂. Crossed March 18, 1897. Pod ripened August 15, 1897; 166 healthy seeds. (*Orch. Rev.* v. p. 365.)

(4) *Paphiopedium Exul* ♀ × *Cypripedium Calceolus* ♂. Crossed April 16, 1897. (Since ripened 597 good seeds. *Orch. Rev.* v. p. 365.)

(5) *Angræcum sesquipedale* ♀ × *Lælia purpurata* ♂. Crossed May 9, 1897. Fine pod 4½ inches in girth, opened July 30, 1897, eighty-two days after pollination; no seeds, ovules shrivelled. Interior of the pod full of fluffy, silky, downy threads or fibres, loosely woven together.

(6) *Cattleya Mossiae* ♀ × *Angræcum sesquipedale* ♂. Crossed May 9, 1897. Pod swelled to 2¼ inches girth; withered away, July 1, 1897. Pollen tubes had grown 2½ inches down the column, and had reached the ovary; ovules undeveloped.

Since then I have set two pods of *Oncidium incurvum* ♀ × *Odontoglossum crispum* ♂, swelling rapidly. Crossed August 11, 1897².

A summary of my notes was republished in M. Cogniaux's *Dictionnaire Iconographique des Orchidées (Chronique Orchidéenne)*, June 1897, and in the following number M. Georges Mantin, of Château de Belair, Olivet, Orleans, was good enough to give his opinion on

¹ In the light of Mendelism this explanation of 1897 is unnecessary. Further it is now evident that the "prepotency" of *Zygopetalum* is of a different nature from that of the dominance of *Epidendrum*. (*Note added 1914.*)

² Cf. pp. 1-5.

these generic crosses, comparing them with others made by himself on similar lines, such as Paphiopedium \times Phragmipedium, Cypripedium \times Paphiopedium, Cypripedium \times Phragmipedium, Oncidium Papilio crossed with self and with other Oncidiums, Lockhartia \times self, and with Oncidiums, &c. M. Mantin obtained pods and even seeds from these crosses, but had never been able to raise any plants. ("J'ai observé parfois des grossissements prolongés de l'ovaire. J'ai même obtenu des graines de ces croisements plus ou moins rationnels, mais il n'est jamais rien levé de ces semis.") M. Mantin also mentioned that he had sown seeds of more than forty pods of Paphiopedium (Cypripedium) barbatum and allied species crossed with Cypripedium Calceolus, but none ever grew. ("J'ai servi plus de 40 (je dis *quarante*) gousses à graines de C. barbatum et espèces voisines fécondées par C. Calceolus. Je n'ai jamais constaté qu'une seule graine ait germé.") Further, M. Mantin expresses the opinion that in the above curious crosses I shall reap the wind instead of seeds, and will be very lucky if I do not reap the whirlwind also in the death of my plants by submitting them to such a parentage. I must say that I am a little more hopeful in this matter than M. Mantin appears to be, though I stated at the time that "it yet remains to be seen whether these healthy-looking pods will produce good seed." (*Orch. Rev.* v. p. 180.)

True, in one case I have already "reaped the wind," but in another I have reaped *good seeds*, and one success is worth many failures, so that I am looking forward to the future with increased interest. With regard to the health of the plants bearing these seed-pods, I do not find that they have suffered more than is usual with seed-bearing plants, and I hope that the "whirlwind" may be yet a great way off.

Still, I do not think it wise to lay too much stress on the production of pods in these curious generic crosses, for pods are often formed apart from fertilisation or pollination. Darwin in his *Animals and Plants*, i. p. 434, gives a remarkable instance of this. "Mr Smith, late Curator at Kew, observed the singular fact that the development of the ovarium could be effected in the South African Orchid, *Bonatea speciosa*, by the mechanical irritation of the stigma *without any pollen*." The Secretary of the Orchid Committee of the R.H.S., Mr Jas. O'Brien, has had a similar experience with *Lycaste Skinneri* and *Odontoglossum crispum*. (In litt., September 25, 1897.) By placing small pieces of grit on the stigmas of these, he found that the ovaries in many cases swelled, and the pods attained maturity just as though the flowers had been properly fertilised; but of course with no vitality in the grains within. We have already seen

how Dr Hildebrandt and Mr Harry Veitch independently observed that the development of the pod in the ordinary pollination of *Dendrobium* and *Cattleya* takes place long before the pollen tubes have reached the ovules. We also know from experiments that pollen grains will push out pollen tubes in an artificial sugar solution, altogether apart from the stigma; and, further, that pollen grains placed in gelatine at some distance from isolated ovules in the same medium send out their tubes and at once make for the ovules. This has been observed in the case of widely different plants. Thus the pollen tubes of a *Monocotyledon* have been attracted by ovules of *Dicotyledons*, and in some cases have actually penetrated the micropyle itself; but, of course, fertilisation has not taken place. (Kerner and Oliver, *Nat. Hist. Plants*, II. p. 415.) In my own observations in crossing distinct genera of Orchids, *Cattleya* × *Angræcum*, *Dendrobium* × *Epidendrum*, *Dendrobium* × *Cattleya*, *Dendrobium* × *Odontoglossum*, *Epidendrum* × *Odontoglossum*, in many cases the pollen tubes grew, and the pods swelled slightly, but fertilisation did not take place.

In fully formed pods that have opened prematurely, and have been found to be empty, nearly all have had bundles of pollen tubes lying alongside the undeveloped ovules, sometimes extending to the bottom of the pod, but with no traces of fertilisation.

Thus we see that the swelling of the pod and the growth of the pollen tubes may be in a sense mechanical rather than physiological and therefore we should not attach too much importance to the fact that the pod has developed to its normal size after the application of foreign pollen. We should wait until proper fertilisation has taken place and good seeds are produced before venturing to think of success. Even then, if the seeds germinate by proper treatment, and plants are raised, they may refuse to flower, as in many *Paphiopedium* × *Phragmipedium* crosses hitherto; and if they flower they may not turn out to be true hybrids as in the *Zygopetalum* crosses mentioned above. "There's many a slip betwixt the cup and the lip." Nevertheless, whether we succeed or whether we fail, all these experiments and observations are interesting, and add to our knowledge of plant life.

FERTILITY AND STERILITY OF HYBRIDS.

Before Darwin published his *Origin of Species* it was generally held by naturalists that distinct species were seldom fertile with one another, and that if hybrids were raised at all they were quite sterile and barren; and very often the whole question was begged by classing

those species that did cross as varieties of one. Darwin made a most careful and elaborate study of the whole question of hybridism, and came to the following conclusions:—"First crosses between forms sufficiently distinct to be ranked as species, and their hybrids, are very generally, but not universally, sterile....The sterility is of all degrees." (*Origin of Species*, 6th ed., p. 262.) Again: "The sterility of distinct species when first united, and that of their hybrid offspring, graduates by an almost infinite number of steps from zero (when the ovule is never impregnated and a seed capsule is never formed) up to *complete fertility*....This high degree of fertility is, however, rare." (*Animals and Plants*, 2nd ed., vol. II. p. 163.)

Fifteen years later we find Dr Alfred Wallace enunciating similar views. He writes: "One of the greatest, or perhaps we may say the greatest, of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species has been the remarkable difference between varieties and species in respect of fertility when crossed. Generally speaking, it may be said that the varieties of any one species, however different they may be in external appearance, are perfectly fertile when crossed, and their mongrel offspring are equally fertile when bred among themselves; while *distinct species*, on the other hand, however closely they may resemble each other externally, are *usually infertile* when crossed, and their *hybrid offspring absolutely sterile*." (*Darwinism*, 1890, p. 152.) Dr Wallace wrote these words some years ago, but since that time some hundreds of hybrid Orchids raised by hand from distinct species have flowered in gardens.

In consulting that admirable work of reference, the *Orchid Hybrids*, by Mr George Hansen, of California, with the second supplement made up to April 1, 1897, I find that there are on record 733 hybrids from *distinct crosses* which have already flowered, and of these 485 are the offspring of species \times species, and the remainder, 248 in number, are all the offspring of hybrids.

As far as the great Orchid Order is concerned, therefore, we can hardly say now that "distinct species...are usually infertile when crossed," and still less can we say that "their hybrid offspring are absolutely sterile."

Darwin laid much stress on the different degrees of sterility, almost as much as on absolute sterility. In Orchids we have not yet sufficient evidence to show that crosses between distinct species produce fewer offspring than crosses between varieties of the same species; or, on the

contrary, that they are equally fertile, very few of the latter crosses having been attempted; and as it is with species so it is with hybrids.

In the meantime perhaps the following figures will give us an idea as to the relative fertility of species and hybrids in the *Cypripedium* group. These figures are taken from the records kindly placed at my disposal by Mr Reginald Young, of Sefton Park, Liverpool, and have been carefully copied by him from his stud-book with his well-known care and precision.

Taking the *Paphiopediums*, or East Indian *Cypripediums*, which broadly represent the tropical species of this group in the Old World (Rolfe, in *Orchid Review*, IV. p. 363), I find that in five years Mr Young has made 577 crosses among thirty distinct species, and fifty-three distinct hybrids, crossing species with species, species with hybrids, hybrids with species, and hybrids with hybrids, and all under uniform conditions. Out of these 577 crosses Mr Young succeeded in getting 452 pods of good seed, which represents 78·3 per cent. fertile. An analysis of these figures shows that out of 188 crosses between distinct species 179 pods of good seed were obtained: a degree of success difficult to excel even in crosses between varieties of the same species, representing as it does 95·2 per cent. fertile: while out of 389 crosses in which a hybrid was concerned in the parentage 273 pods of good seed were obtained, being 71·8 per cent. fertile, showing a decrease of fertility of 23·4 per cent. in crosses between hybrids as compared with crosses between species. This seems to point to the conclusion that in this *Cypripedium* group while crosses between distinct species are almost, if not quite, as fertile as crosses between varieties of the same species, yet crosses with hybrids, though fertile to a very large extent, are yet *slightly less* fertile than crosses between species. What is the cause of, this slight decline in the fertility of hybrids? From Mr Young's experiments it seems to be due in a large measure to the loss of power in the male element of the hybrid. For out of 143 hybrids crossed with the pollen of pure species 128 fertile pods were obtained, or 89·5 per cent., showing a very slight loss of power in the female element of the hybrids of 5·7 per cent.: while out of 118 pure species crossed with the pollen of hybrids only sixty-seven pods of good seed were obtained, showing 56·7 per cent. fertile. This represents a loss of power in the male element of the hybrids of 38·5 per cent. compared with that of species crossed with species. Why the male element should be affected more than the female element in hybrids is not at all clear; and whether in time by constant crossing this would

gradually be eliminated I cannot say ; but I observe that while species crossed with pollen of hybrids produce as we have seen 56·7 per cent. fertile pods, yet 124 hybrids crossed with pollen of hybrids produced seventy-four good pods, or 59·6 per cent., being an increase of fertility of 2·9 per cent. This may possibly be due to the fact that the hybrids crossed with hybrids were of necessity more nearly related to one another than species crossed with hybrids, and it is highly probable that by constant mixing hybrids may regain the higher fertility usual among species and varieties.

The lessened fertility of hybrids used as the male parent compared with the greater fertility of hybrids used as the female parent, and its probable effect on the intercrossing of species in a state of nature, are not for me to deal with now ; but it is of great importance to the evolutionist as a possible factor in the origin of species. All these experiments and observations prove to us how important it is for Orchid breeders to keep accurate and precise records of the crosses they make from time to time, the details of which may prove to be of inestimable value to science.

III

CURIOSITIES OF ORCHID BREEDING¹

A few years ago the raising of hybrid Orchids was entirely in the hands of a few English experts, but quite recently it has been taken up with great success by many growers of these rare and beautiful plants, not only in England, but also on the Continent and in America.

Consequently Orchid hybrids have become very numerous, while new ones are constantly being brought to light. Up to the year 1860, we find but four flowered hybrids recorded, raised from distinct crosses: during the thirty years following the numbers gradually increased, until in 1890 there were about 200 enumerated. But it is in the present decade that the most rapid strides have been made, the numbers having increased by leaps and bounds until at the present time there are on record no less than 800 Orchid hybrids, raised by hand from distinct crosses. These have all flowered in gardens, and have been duly described or recorded in various journals. And when we remember that many of these 800 crosses have been repeated in the same garden, and in other gardens, and that many individual plants may have been obtained from each capsule, we can form an idea of the large number of hybrid Orchids that have been raised by hand.

PRIMARY HYBRIDS.

Of the 800 hybrids from distinct crosses, now on record, some 500 are primary hybrids, *i.e.* hybrids of the first generation between two different species. A careful examination of these primary hybrids shows that, as a rule, they are fairly intermediate between their parents, partaking of the characters of both, and at the same time perfectly distinct from either. The latter fact is most remarkable, and

¹ Reprinted from *Nature*, LIX. (1898), pp. 178-181.

at once serves to distinguish primary hybrids clearly from all other hybrids. For example, *Cypripedium* \times *Leeanum* (figs. 5, 24) is a typical primary hybrid, and has perhaps been raised more frequently and in larger numbers than any other Orchid hybrid. It was obtained originally by crossing *C. insigne* (Wallich), ♀ (figs. 9, 25), with *C. Spicerianum* (Rehb. f.), ♂ (fig. 6), both well marked and distinct species. The hybrid is fairly intermediate both in its outward characters and in its inner structure (see Prof. Macfarlane on "Minute Structure of Plant Hybrids," *Trans. Roy. Soc. Edin.*, 1891, XXVII. p. 245), and although it has innumerable minor and individual variations, yet it is always perfectly distinct from both of its parents.

Nor has any intrinsic difference been observed in the reciprocal cross, the same forms appearing equally in the obverse and reverse crosses. Often many varieties are obtained from the same capsule, differing slightly in colour, form and size, but all are specifically *C. \times Leeanum*, and cannot be mistaken for anything else (fig. 24). As it is with *C. \times Leeanum* so it is with many other primary Orchid hybrids, so far as experiments have been made. In short, we find that primary hybrids are, as a rule, so intermediate between their parent species, and so comparatively uniform in character, that they are specifically distinct from both parents.

GENERIC HYBRIDS.

Of the 500 primary hybrids on record, about 100 are generic hybrids, *i.e.* the parents belong to different genera. In this respect alone these hybrids are interesting, though no doubt the systematic botanist views them with mixed feelings. It is not so long since generic hybrids were looked upon as anomalies; some of the older naturalists even regarded them as impossible, and forthwith proceeded to beg the whole question by classing those genera, which were fertile with one another as species of one. Orchid growers, at all events, have almost ceased to regard generic hybrids with curiosity, familiarity with them having bred a certain amount of indifference.

A list of the generic hybrids on record up to the end of 1897, together with a diagram showing how twenty-six different genera have been linked together by artificial hybridisation, has been prepared by the writer and was published in the *Journal* of the Royal Horticultural Society (vol. XXI., April 1898), to which those interested in the details of generic orchid hybrids may be referred. (See p. 27.)

Generally speaking, primary generic hybrids follow the rule of specific hybrids in bearing the intermediate characters of their parents, with a narrow range of variation.

But there are a few remarkable exceptions to this rule.

(1) *Epiphronitis* × *Veitchii*, a hybrid out of *Sophranitis grandiflora* (Lindl.) by *Epidendrum radicans* (Pav.).

(2) *Epi-Cattleya* × *matutina* (fig. 44), a hybrid out of *Cattleya Bowringiana* (Veitch) by *Epidendrum radicans* (Pav.) (fig. 46).

(3) *Epi-Laelia* × *radico-purpurata*¹, a hybrid out of *Laelia purpurata* (Lindl.) by *Epidendrum radicans* (Pav.).

(4) *Epi-Laelia* × *Charlesworthii*, a hybrid out of *Laelia cinnabarina* (Lindl.) by *Epidendrum radicans* (Pav.).

These four generic hybrids are very curious indeed, inasmuch as all agree in reproducing the generic characters only of the pollen parent *Epidendrum*, without the slightest trace of the peculiar structure of the seed-parents, *Sophranitis*, *Cattleya* and *Laelia*. Yet in minor characters, in colour, form and size, the four hybrids distinctly differ from one another and from their *Epidendrum* parent.

A close examination reveals the fact that these minor differences correspond with the peculiar differences in the parentage, thus showing that the crosses have really been effected: yet at the same time it must be candidly admitted that did we not know the parentage, we could never have determined it, so overwhelming is the influence of the predominant partner *Epidendrum radicans*. It will, no doubt, be observed that *E. radicans* is the pollen parent in each of the above cases. Curiously enough, when this reed-like *E. radicans* is crossed with the pseudo-bulbous *E. vitellinum* (Lindl.), ♀, a similar result is obtained, the offspring *E. × radico-vitellinum*² being scarcely distinguishable from the reed-like *E. radicans*. Again, when the reed-like *E. × O'Brienianum*—itself a hybrid out of *E. evectum* (Hook. f.) by *E. radicans*—is crossed with the pseudo-bulbous *E. vitellinum*, ♀, a similar result is obtained, the offspring being reed-like in habit as in the pollen parent³. Yet when the reed-like *E. radicans* is crossed with other reed-like species of *Epidendrum*, and again when the pseudo-bulbous species of *Epidendrum* are crossed with species of *Laelia*, in every case normal hybrids are produced intermediate between their parents.

¹ Now named *Epilaelia Veitchii* (fig. 45). (Note added 1914.)

² Now named *Epidendrum Cassiope*. (Note added 1914.)

³ This hybrid is named *E. Phæbus*, *Orch. Rev.* vi. (1898), p. 169. (Note added 1914.)

Though we cannot pretend to unravel this tangled skein, yet, so far as experiments have been made, it seems quite clear that

(1) The species of *Cattleya*, *Laelia*, *Sophronitis*, and the pseudo-bulbous species of *Epidendrum*, when intercrossed, produce normal hybrids intermediate in character.

(2) The same result is obtained when the reed-like species of *Epidendrum* are united with one another.

(3) But when the reed-like species of *Epidendrum* are united with the pseudo-bulbous species of *Epidendrum*, or with species of *Cattleya*, *Laelia* and *Sophronitis*, abnormal hybrids are produced, having the essential characters of the reed-like *Epidendra*. From these facts it might easily be argued that a reed-like *Epidendrum* was the ancestor not only of the pseudo-bulbous *Epidendra*, but also of the more highly specialised genera *Cattleya*, *Laelia* and *Sophronitis*. In that case the pseudo-bulbous *Epidendra* would form an interesting connecting link between the lowly reed-like *Epidendra* and the gorgeous aristocratic *Cattleya* and *Laelia*. (Cf. pp. 34, 35.)

PREPOTENT GENERIC CROSSES.

Perhaps the strangest curiosity in the history of orchid hybridisation is the remarkable prepotency of the genus *Zygopetalum* over the three genera *Odontoglossum*, *Oncidium* and *Lycaste*, so far as experiments have been made. *Zygopetalum Mackayi* (Hooker) has been crossed with four distinct species of *Odontoglossum*, viz. *O. Pescatorei* (Linden), *O. crispum* (Lindl.), *O. grande* (Lindl.) and *O. bictonense* (Lindl.), also with one species of *Oncidium*, *O. unguiculatum*, and one species of *Lycaste*, *L. Skinneri* (Lindl.), by more than one hybridist, and the result has always been the same, namely *Zygopetalum Mackayi* pure and simple, without a trace of the peculiar structure of the pollen parent in any case. This result is very perplexing and exceedingly difficult to account for. I have made careful inquiries into the details of all these cases, and have satisfied myself that accidental self-fertilisation is out of the question, the pollen of the mother parent having been carefully removed in every case previous to pollination. Parthenogenesis, too, is evidently a broken reed to lean upon, for the seedlings from the same seed-pod differed among themselves in colour and other minor characters, which would hardly have been the case had they arisen from parthenogenetic seed-buds. (See 1914 footnote, p. 36.) Neither is *Z. Mackayi* naturally prepotent over other species when

crossed, there being at least three cases to the contrary. Nor is the genus *Zygopetalum* naturally prepotent over other genera, as two distinct and intermediate hybrids between *Zygopetalum* and *Colax* testify. As in the case of the *Epidendrum* crosses, mentioned above, it may be suggested that *Zygopetalum* is the ancestral genus of *Odontoglossum*, *Oncidium* and *Lycaste*, and that the characters of the ancestral genus remain latent in the more recent genera, with the result that when the latter are crossed with the former, the mixing of the germ-plasms causes these original characters to dominate, the outcome being a reversion to the ancestral genus *Zygopetalum*.

A rather interesting fact has come to light which certainly lends colour to the above speculation: The seedling *Odontoglossums*, raised in the gardens of Baron Rothschild, of Paris, during the first eighteen months of their growth, are said to have resembled *Zygopetalum* more than they did *Odontoglossum*. This coincides with the established fact that living beings tend to resemble their ancestors in the early stages of their development. However, for the present we must suspend our judgment, and wait patiently for further facts: it is to be hoped that future experiments will throw more light upon these curious generic crosses.

Another curious fact in connection with generic crosses may perhaps be of interest, and that is the remarkable crosses between the East Indian species of *Cypripedium* and the South American species: these two sections of the old genus *Cypripedium* have recently been raised to generic rank, under the names of *Paphiopedium* and *Phragmipedium* respectively, by Mr R. A. Rolfe, of Kew, and seem to form two distinct and natural groups. Hybrids between these two new genera are peculiarly interesting, inasmuch as the former has a one-celled ovary, while the latter has a three-celled one, showing that this condition is no barrier to fertilisation. More than twelve distinct crosses between different species of these two genera are on record, and many plants have been raised, but so far all resolutely refuse to flower, notwithstanding the many inducements that have been put in their way, and many of them are now large vigorous plants, long past the usual flowering age. One plant of these crosses is recorded to have flowered in the United States, but as it flowered exactly the same as the mother plant in genus, species and variety, one cannot be quite sure that the cross was really effected.

Many of the remaining plants (the writer has several in his

collection) are distinctly intermediate in their foliage and habit of growth, and clearly bear the stamp of their recorded origin.

SECONDARY AND TERTIARY HYBRIDS.

Of the 800 distinct crosses mentioned in the foregoing, some 270 are secondary hybrids, *i.e.* hybrids of the second generation, one or both parents being a primary hybrid; while thirty are tertiary hybrids, *i.e.* hybrids of the third generation, one of the parents, at least, being a secondary hybrid. So far no hybrid orchids are recorded to have flowered beyond the third generation, but perhaps it may not be premature to mention that unflowered hybrids of the fourth generation are known to be in existence. The writer has in his collection six hybrids of the fourth generation, five years old, all raised from the same capsule, which contain in their pedigree five distinct species and three distinct hybrids, so that in the near future there will be ample material in this direction at the disposal of the student of heredity; with this distinct advantage, that orchids being individually valuable, their pedigree is carefully and systematically recorded, which unfortunately is more than one can say of the great majority of garden hybrids.

A careful examination of secondary hybrids shows them to be very different from primary hybrids in their range of variation. As we have already seen, primary hybrids are comparatively uniform in their characters; so much so that, as a rule, they are quite distinct from their parents. On the other hand, secondary hybrids have a much wider range of variation, often approaching either parent, and sometimes even reverting wholly to one or the other. For instance, to take the simplest form of a secondary hybrid, *i.e.* a hybrid crossed with one of its parent species, we find that the offspring, as a rule, are very variable, a few reverting to the parent species and a few to the parent hybrid; but the great majority are intermediate forms approaching either parent, the whole forming a series of links between one parent and the other. In short, we find that secondary hybrids have a far wider range of variation than have primary hybrids. (Cf. figs. 24—28.)

NATURAL HYBRIDS.

The existence of natural hybrids was formerly thought by some naturalists to be highly improbable, if not actually impossible, but now, when absolute facsimiles of supposed natural hybrids have been

raised by hand in gardens, from the same two species among which they naturally grow, they can no longer be regarded as pious speculations, but are indeed accomplished facts (figs. 54—56). The number of proved natural hybrids in orchids alone is now very considerable, with the result that many intermediate and doubtful forms, hitherto classed as distinct species, are now placed in their proper position as natural hybrids. Mr R. A. Rolfe, of Kew, has done yeoman service in reducing the chaos of natural hybrid orchids to something like order. *And so it has come to pass that artificial hybridisation, which it was supposed would lead systematic botany into the direst confusion, by the irony of fate, seems destined to be the only trustworthy means of saving systematic botany from its own confusion;* and the systematist, however orthodox he may be, can no longer afford to ignore artificial hybrids.

FERTILITY OF HYBRIDS.

The question of the fertility of hybrids is a highly interesting one, and especially important to the student of evolution; and I venture to think that recent experiments in orchid hybridisation have added considerably to our knowledge of the subject.

One of the principal objections to Darwin's theory of the origin of species was the supposed general sterility of hybrids.

Darwin fully appreciated this difficulty, and, after a careful and most elaborate survey of the whole question of hybridism, came to the following conclusions: "First crosses between forms sufficiently distinct to be ranked as species, and their hybrids are very generally, but not universally sterile....The sterility is of all degrees" (*Origin of Species*, 6th ed. p. 262). Again: "The sterility of distinct species, when first united, and that of their hybrid offspring, graduates by an almost infinite number of steps from zero (when the ovule is never impregnated, and a seed capsule is never formed) up to complete fertility. ...This high degree of fertility is, however, rare" (*Animals and Plants*, 2nd ed. vol. II. p. 163). Some fifteen years later, Dr Alfred Russel Wallace took up a somewhat similar but more definite position. He writes: "One of the greatest, perhaps we may say the greatest, of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species, has been the remarkable difference between varieties and species in respect of fertility when crossed. Generally speaking, it may be said that the varieties of any one species, however different they may be in external appearance,

are perfectly fertile when crossed, and their mongrel offspring are equally fertile when bred among themselves; while distinct species, on the other hand, however closely they may resemble each other externally, are usually infertile when crossed, and their hybrid offspring absolutely sterile" (*Darwinism*, 1890, p. 152). Since that time, hundreds of hybrid orchids have been raised in gardens; as we have already seen, there are now on record some 500 distinct primary hybrids raised from distinct species, also some 300 secondary and tertiary hybrids from distinct crosses, raised from parents themselves hybrids.

In the face of these facts, therefore, we can hardly maintain that "distinct species...are usually infertile when crossed," and still less can we assert that "their hybrid offspring are absolutely sterile." As it is with orchids, so it is with other garden plants that have been hybridised, *e.g.* roses, rhododendrons, dahlias, chrysanthemums, carnations, begonias, pansies, &c.: the wonderful forms seen in gardens at the present day are all hybrids of many generations, being the known product of more than one species; and these are all fertile in the production of seeds. Darwin seemed to attach much importance to the different degrees of fertility in hybrids ranging from complete fertility down to absolute sterility. At present we have no means of ascertaining the relative fertility of hybrid orchids with that of ordinary species, owing partly to the fact that very few crosses have been made in gardens between varieties of the same species, and partly to the fact that many thousands of seeds are contained in one capsule, being practically innumerable, but through the kindness of Mr Reginald Young, of Liverpool—an enthusiastic connoisseur in *Cypripediums*—the writer has been able to work out certain statistics bearing on the question of the comparative fertility of hybrids (see *Journ. Roy. Hort. Soc.* vol. XXI. April 1898).

The voluminous records in Mr Young's stud-book cover a period of about five years, and were specially selected by the writer on account of the reputation of the breeder as a careful observer and a precise recorder. Out of the 577 crosses made by Mr Young among thirty distinct species and fifty-three distinct hybrids of the new genus *Paphiopedium*, no less than 78·3 per cent. proved fertile, *i.e.* produced good seeds.

Of these, the crosses between distinct species only, 95·2 per cent. were fertile, while the crosses in which a hybrid was concerned in the parentage 71·8 per cent. proved fertile.



Fig. 54. *Lælia purpurata* Lindl.

Fig. 56. *Cattleya intermedia* Graham.

Fig. 55. \times *Læliocattleya Schilleriana* Rolfe.

A natural generic hybrid with its parents, from the Santa Catherina district of South Brazil. This hybrid has been raised artificially three times and its parentage confirmed.



Fig. 57. ×*Odontoglossum Andersonianum* Rehb. f.

Showing 12 forms of the Natural Hybrid from *O. gloriosum* Rehb. and *O. crispum* Lindl. from the Cordilleras of Colombia, and illustrating the variability of natural hybrids. The top row have clear white grounds, the second row have cream grounds suffused with rose, the third row have clear yellow grounds, and the bottom row have yellow grounds suffused with rose. The parent *O. gloriosum* has small, yellow, densely spotted flowers. The parent *O. crispum* has large, white flowers suffused with rose and lightly spotted.

This seems to show that crosses between distinct species are almost if not quite as fertile as crosses between varieties of the same species (taking the latter at complete fertility, *i.e.* 100 per cent.); while crosses with hybrids, though fertile to a high degree, are yet rather less fertile than crosses between species. A further analysis of the figures shows that while hybrids crossed with pollen of pure species give 89.5 per cent. fertile, yet pure species crossed with pollen of hybrids give but 56.7 per cent. fertile. This points to the conclusion that the slight decline in the fertility of hybrids is due in a large measure to the loss of power in the pollen of hybrids.

Why the male element in hybrids should be so much less potent than the female element I cannot pretend to say, but I venture to think that the matter is worthy of consideration as a possible factor in the evolution of species.

EVOLUTION OF SPECIES BY NATURAL HYBRIDISATION.

The experimental demonstration of natural hybrids shows clearly that intercrossing between different species is carried on in a state of nature, to a far greater extent than was formerly supposed; and the comparative fertility of these natural hybrids would be of vital importance to them in their struggle for life.

If, as seems highly probable from the above experiments with orchids, it is the pollen only of hybrids that is impaired, and the capacity of the hybrid to bear seed crossed with the pollen of pure species remains practically unimpaired, it is quite clear that the natural hybrid has a part to play in the evolution of new species.

As we have already seen, hybridisation tends to increase variation especially beyond the first generation, and, naturally, the more variable the offspring the better fitted would they be to adapt themselves to changed conditions of life (fig. 57).

If the circumstances changed rapidly and considerably, the variable offspring of the hybrids would stand a better chance in the struggle for life than the more uniform offspring of the parent species, which were themselves specially adapted to the old conditions. In this way, as conditions changed, new species would be evolved more fitted to the new conditions of life than the old species, which they would gradually replace, and I venture to suggest that natural hybridisation is the most rapid of nature's means towards that end.

IV

NOTES ON SOME EXPERIMENTS IN HYBRIDISATION AND CROSS-BREEDING¹

During the past few years the question of inheritance has been of increasing interest to students of Evolution as well as to the practical breeder.

Since the foundation-stone of the subject was laid by Charles Darwin in the standard work, *Animals and Plants under Domestication*, our knowledge of one part of it has considerably increased. Thanks to recent improvements in the mechanism of the microscope, and the consequent facilities for studying the inner processes of fertilisation, the tendency has been for students of heredity to give most of their attention to the mysteries of the germ-cells and the part they play in sexual reproduction. This is, undoubtedly, very desirable and very necessary; yet, on the other hand, there seems to be a danger that in so doing we may lose sight of the broad facts of inheritance as manifested to us in the outward characters of plants and animals. And it seems to me that, notwithstanding the great body of facts already brought together by Darwin in his magnificent work, there is still a wide field open to the student in making further experiments and in gathering fresh facts.

The aim of this paper is to record, as concisely as possible, some experiments in the hybridisation and cross-breeding of plants, carried out by myself and others, which seem to bear directly upon the problems of inheritance and variation.

THE INHERITANCE OF VARIETAL CHARACTERS.

From the horticultural point of view, the inheritance or non-inheritance of varietal characters is most important. If a useful or ornamental variety is capable of transmitting its good qualities to its

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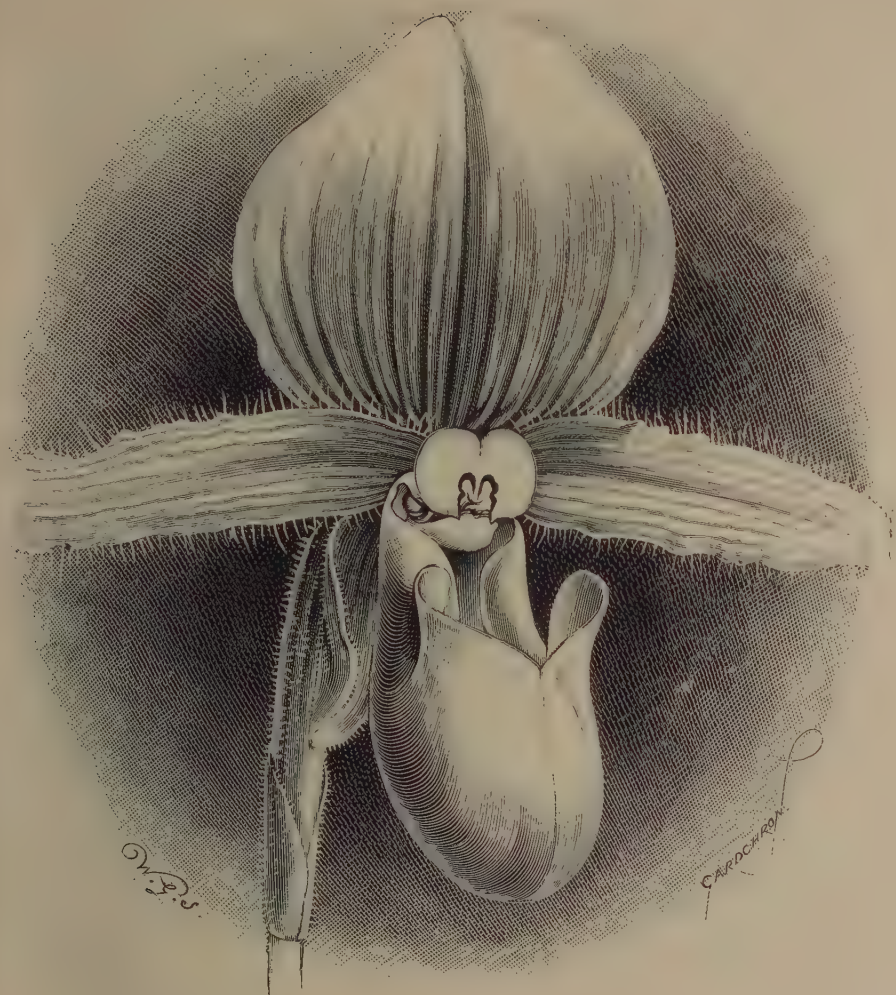


Fig. 58. *Paphiopedilum Lawrenceanum* Pfitz. var. *Hyeaenum* Hurst.
Showing a flower of one of the albinos raised by Mr Norman Cookson.
(*Gardeners' Chronicle*.)



Fig. 59. *Paphiopedilum insigne* Pfitz. var. *Sanderæ* Rolfe.

A yellow variety of the type.

(*Orchid Review*).

offspring, then its own natural value becomes greatly enhanced, and in the course of a few generations a more or less permanent race may be established. Most breeders have a strong impression that varieties possess the power of transmitting their qualities to their offspring, and in practice they take care to breed only from the best which suit their purpose, in the hope that the improvement may be maintained, and, if possible, increased; but, having observed many exceptions to this general rule, in the Orchideæ, I have thought it worth while to consider the question somewhat in detail. Take, first of all, a natural variety fertilised with its own pollen; in this case, if a varietal character be hereditary at all, it should, *à priori*, be especially so when fertilised with its own pollen. *Paphiopedilum Lawrenceanum* Hyea-num is an albino form of the type, in which all the purple and brown colouring matter is suppressed, leaving the whole plant shades of green and white. Mr Norman Cookson, of Wylam-on-Tyne, fertilised this variety with its own pollen, and a batch of seedlings was raised (fig. 58).

The first eight plants that flowered reproduced exactly the characters of the parental variety, *P. L. Hyea-num*, but the ninth one is said to have reverted to an ordinary form of the type *P. Lawrenceanum*¹.

P. insigne Sanderæ is a variety in which nearly all the brown and green colouring matter of the type has vanished, leaving the variety shades of yellow and white. Mr Norman Cookson has also raised this true from self-fertilised seed (fig. 59)².

P. ×Harrisianum Rossianum is a striped variety or sport of a light-coloured hybrid between *P. villosum* and *P. barbatum*, in which the colours of the two parents, in the flowers, lie side by side, instead of being fused together as in the type, giving the variety a curious harlequin appearance. Mr H. J. Ross, of Florence, fertilised this variety with its own pollen, and the first plant which flowered reproduced the varietal characters faithfully, while the second one reverted to the light-coloured original form.

¹ This apparent exception is so far unique, and quite inexplicable in view of recent results with selfed "albinos". (Note added 1914.)

² These plants were "true" in the sense that all were *yellow* forms of the type, but the individuals raised from the same seed-pod varied considerably in form, size, and in the amount of brown dotting on the dorsal sepal of the flower. Further, out of five seedlings of *P. i. Sanderæ* raised by Messrs Veitch from selfed flowers, two had no brown dotting at all, being apparently true albinos like *P. i. Sanderianum* (Rolfe in *Orch. Rev.* xviii. (1910), p. 350). (Note added 1914.)

Dendrobium nobile Cooksonianum is an abnormal variety, with the petals coloured somewhat as in the lip (irregular peloria). This variety was crossed by Mr Cookson with *D. n. nobilius*, a variety with deep purple sepals and petals; and from the same seed capsule were raised both *D. n. Cooksonianum* and *D. n. nobilius* true to character, together with a series of reversionary forms grading down to the ordinary type of *D. nobile*.

On the other hand, Mr Fred Hardy, of Ashton-on-Mersey, crossed a large form of the typical *D. nobile* with pollen of *D. n. Cooksonianum*, and, though the seedlings resulting therefrom varied considerably, not one had the characteristics of *D. n. Cooksonianum*.

Again, Mr Cookson crossed *D. n. Cooksonianum* with pollen of *D. n. burfordiense*; the latter being a variety with the two lower sepals coloured like the lip, instead of the petals, as in *D. n. Cooksonianum*. One of these seedlings reproduced *D. n. burfordiense* truly.

Mr Cookson also crossed *D. n. burfordiense* with a distinct species, *D. Findlayanum*, and raised a hybrid known as *D. × Cybele* Oakwood, and all the plants reproduced the characteristic blotch on the lower sepals as in *D. n. burfordiense* (fig. 60). Both *D. n. Cooksonianum* and *D. n. burfordiense* are technically anomalies, being cases of irregular peloria; and they seem to reproduce their sportive characters in their offspring either wholly or not at all, there being no intermediate forms between them and the normal¹.

D. × Cybele, Oakwood, mentioned above, is a good illustration of the inheritance of varietal characters, especially when we remember that the typical *D. nobile*, crossed with *D. Findlayanum*, produces the typical *D. × Cybele*; and again, when *D. n. nobilius*, a richly coloured variety of the type, is crossed with *D. Findlayanum*, the result is *D. × Cybele nobilius*, a correspondingly coloured variety of the typical hybrid.

D. nobile crossed with *D. Falconeri* produces the typical *D. × Venus*, but when *D. n. nobilius* is used as one parent *D. × Venus magnificum* is produced, its colour being correspondingly deeper than the type.

D. nobile crossed with *D. aureum* gives the typical *D. × Ainsworthii*; but Messrs Veitch & Sons, of Chelsea, by using special varieties of each species as parents, produced *D. × Ainsworthii splendidissimum*, a greatly improved form. On the other hand, a partial

¹ The genetic behaviour of these peloriate forms of *Dendrobium nobile* is not at all clear, and an investigation of them on Mendelian lines might yield results of considerable importance. (*Note added* 1914.)

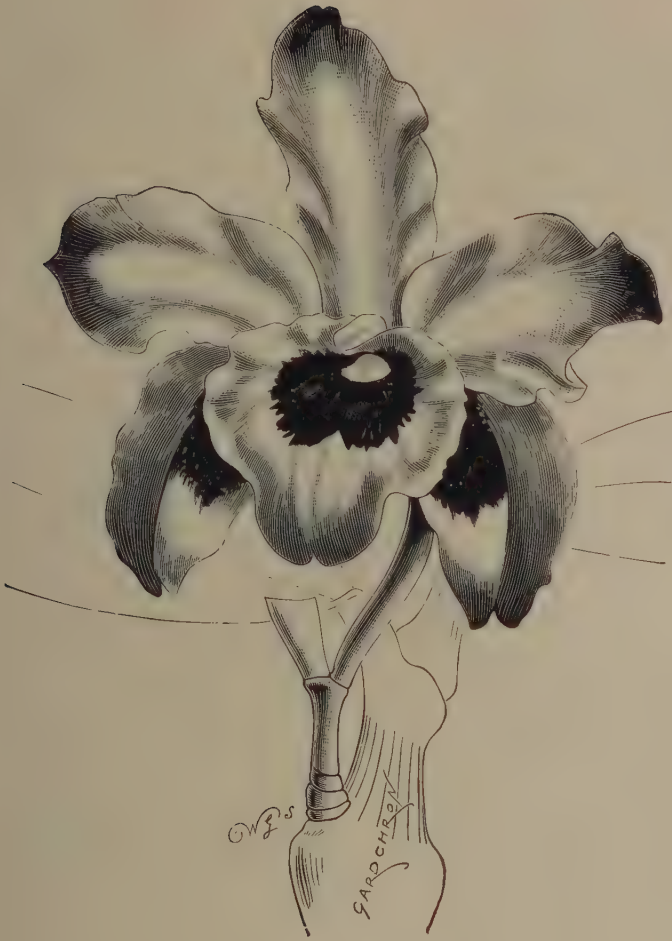


Fig. 60. × *Dendrobium Cybele* Rolfe var. *Oakwood* Hort. Cookson.
 A peloriate hybrid raised from the peloriate *D. nobile* Lindl. var. *burfordiense*
 Hort. Lawrence and the normal *D. Findlayanum* Parish et Rchb.
 (*Gardeners' Chronicle*.)



Fig. 6r. × *Paphiopedilum Leeanum* var. *superbum* Hurst.
Raised from *P. Spicerianum* (fig. 6) and *P. insigne Chantinii* (fig. 9).
From a photograph taken at Burbage.



Fig. 62. *Paphiopedilum insigne* Pfitz. var. *giganteum* Hurst.

(*Orchid Review.*)

exception may be quoted where *D. n. nobilius*, crossed with *D. aureum*, produced *D. × Ainsworthii Edithæ*, a light-coloured form of *D. × Ainsworthii splendidissimum*, inheriting the form of *D. n. nobilius*, but not the colour.

Mr Cookson crossed the typical *D. nobile* with the typical *D. × Ainsworthii*, and raised a light-coloured form called *D. × Apollo*.

Mr J. Cypher, of Cheltenham, and Mr C. Winn, of Birmingham, crossed *D. n. nobilius* with *D. × Ainsworthii splendidissimum*, and raised the correspondingly deep-coloured *D. × Rubens*; while the Hon. Oakes Ames, of Massachusetts, raised an almost identical hybrid from the reverse cross; but, on the other hand, Mr R. B. White, of Ardarroch, raised a rosy-coloured form of *D. × Rubens*, nearer to the type, from the same cross.

Again Baron Schröder crossed *D. n. Schröderianum*, a variety with white sepals and petals, with *D. × Ainsworthii splendidissimum*, which produced *D. × R. dellense*, also with white sepals and petals, and Mr Cypher crossed *D. n. pulcherrimum*, also a variety with white sepals and petals, with *D. × Ainsworthii splendidissimum*, which produced *D. × R. Apollo* and *D. × Apollo grandiflorum*, both with white sepals and petals.

The original *D. Wardianum* from Assam, with slender pseudo-bulbs, crossed with *D. lituiflorum* by Messrs Veitch, gave *D. × micans* with slender pseudo-bulbs, whereas the modern *D. Wardianum* from Burma, with stout pseudo-bulbs, gives *D. × micans* with pseudo-bulbs correspondingly stout.

Varietal characters seem also to be generally inherited in the *Cypripedium* group; for instance, *Paphiopedilum insigne* crossed with *P. Spicerianum* produced the typical hybrid *P. × Leeaenum*, with Sir Trevor Lawrence; but when *P. i. Maulei* or *P. i. Chantinii* (fig. 9) were used as parents by Messrs Veitch and Mr Winn, *P. × Leeaenum superbum* (fig. 61) was the result, the offspring in these cases corresponding with the parents' varieties in having a larger area of pure white, and being much broader in the upper sepal of the flower. Again, when the densely spotted *P. i. Wallacei* was used as a parent by M. Jules Hye-Leyssen, of Ghent, the densely spotted *P. × Leeaenum Albertianum* was the result; while the yellow *P. i. Sanderæ* (fig. 59) gave with Messrs Veitch the yellowish *P. × Leeaenum Prospero*, and the large *P. i. giganteum* (fig. 62) gave with Messrs Heath, of Cheltenham, the large *P. × Leeaenum giganteum*. Finally, *P. i. Chantinii* crossed with *P. Spicerianum roseum* gave with Hon. Erastus Corning, Albany, U.S.A., the richly coloured *P. ×*

Leeanum roseum. In the same way, the typical *P. insigne* crossed with *P. villosum* gives *P. × nitens Sallierii*, while *P. i. Chantinii* and *P. i. Maulei* give *P. × nitens*, *P. × n. superbum* (fig. 10), *P. × n. Celeus*, and *P. × n. giganteum*; all being superior forms, showing clearly the larger flowers, broader upper sepal, and white area of the parent varieties. Similarly, the typical *P. insigne* crossed with *P. barbatum* gives the typical *P. × Ashburtonia*, while the variety *P. i. Chantinii*, with M. Bauer, of Paris, gave *P. × A. Barteti* and *P. × A. Laforcadei*, both showing the varietal characters of the parental variety. In the same way, the typical *P. insigne*, crossed with *P. Fairieanum*, gave with Messrs Veitch the typical *P. × Arthurianum*; but when their Mr Seden used *P. i. Chantinii* as the parent, the result was *P. × A. pulchellum*, in which the characters of the parental variety are marked. Again, the typical *P. barbatum* crossed with *P. bellatulum*, with several raisers, has given the typical *P. × Richmanii*, with nearly horizontal petals, while *P. barbatum* Crossii, with drooping petals, when used as the parent in this cross, has given *P. × R. Laysenianum*, *P. × R. "François Peeters,"* and *P. × R. "Lilian Greenwood,"* all with pendent petals.

Two apparent exceptions to the above may be cited: *P. b. Crossii* crossed with *P. Charlesworthii* gave *P. × barbato-Charlesworthii*¹, with nearly horizontal petals, and *P. b. Crossii* crossed with *P. Spicerianum* gave *P. × Eyermannianum* Hermione, with nearly horizontal petals.

P. Boxallii crossed with *P. hirsutissimum* by Mr Cookson gave the typical *P. × Godseffianum*, but the dark-coloured variety *P. B. atratum*, used by M. Desbois, gave the dark-coloured *P. × G. Jupiter*. In the same way *P. Boxallii* crossed with *P. Spicerianum*, by Messrs Veitch, gave the typical *P. × Calypso*, while *P. × B. atratum*, used by Mr Winn and Mr Cookson, gave the darker forms, *P. × C. Winn's var.*, *P. × C. Armstrongianum*, and *P. × C. Oakwood var.* Similarly *P. Boxallii*, crossed with *P. barbatum*, gave *P. × apiculatum*, while *P. B. atratum* gave *P. × a. atratum*.

In another section of the *Cypripedium* group the inheritance of varietal characters still holds good to a large extent. For instance, *Phragmipedium Schlimii* crossed with *P. longifolium*, with Messrs Veitch, gave the typical *P. × Sedenii* (the reciprocal cross, too, being exactly the same), whereas *P. Schlimii albiflorum*, with light-coloured flowers, gave *P. × Sedenii candidulum*, with light-coloured flowers; while *P. Schlimii*, crossed with *P. longifolium* Roetzlii, with dark-

¹ Now named *P. × Lumsdenii* Rolfe et Hurst, *Orchid Stud-Book*, 1909, p. 178. (Note added 1914.)



Fig. 63. *Phragmipedium caudatum* var. *Wallisii* Hurst.
A pale form of the species from Ecuador with a normal lip.
(*Orchid Review*.)

Fig. 65. \times *Phragmipedium grande* Rolfe
var. *macrochilum* Hurst.

A hybrid with a normal lip out of the normal
P. longifolium by the lipless *P. caudatum*
Lindenii.

(*Gardeners' Chronicle*.)



Fig. 64. \times *Phragmipedium Schroederæ* Rolfe.

A hybrid with a normal lip out of the normal *P. caudatum*
by the normal \times *P. Sedenii*.

(*Orchid Review*.)

coloured flowers, gave *P. × Sedenii* porphyreum, with dark-coloured flowers. Similarly, *P. longifolium* crossed with *P. caudatum* gave the typical *P. × grande*, while the darker variety, *P. l. Roezlii*, gave the darker *P. × grande atratum*.

One of the most distinct and interesting varieties in the *Cypripedium* group is *Phragmipedium caudatum* Lindenii, a natural peloriate variety so distinct that, when it was first introduced, Lindley created a new genus for it (*Uropedium*). It is peculiar in being lipless, the place of this organ being occupied by a long petal-like segment which sometimes measures twenty inches in length; it has also a third fertile stamen inserted below the stigma at the base of the column (cf. fig. 63). This curious plant was first found growing wild in Rep. Colombia, by the late M. Jean Linden, of Brussels, in 1843, and has since been found by later collectors in other localities, so that apparently it must breed true to character in its own habitat. There is not much doubt, however, that it is simply a peloriate form of *P. caudatum*, for a flower once appeared on a typical *P. caudatum* midway between this curious variety and the type¹. This curious variety, *P. c. Lindenii*, is interesting from another point of view. In its native home it apparently breeds true to character, yet when crossed with other species its curious characters do not appear to be reproduced at all. For instance, it has been crossed with *P. longifolium*, giving *P. × grande macrochilum* (fig. 65); with *P. × conchiferum*, giving *P. × Clonius*; with *P. × Ainsworthii calurum*, giving *P. × Penelaus*; and with *P. × grande*, giving *P. × macrochilum*, and in no case has its curious lipless character been transmitted (cf. figs. 64 and 65). It would be interesting if someone would fertilise this curious variety with its own pollen, or cross it back again with one of the four hybrids of which it has been a parent, and record the result².

Many more instances of inheritance and non-inheritance of varietal characters in the Orchideæ might be recorded, but space will not permit any more. Suffice it to say that a general survey of the whole of the facts has brought me to the following conclusions:—

- (1) Distinct varieties tend to transmit their qualities, especially if fertilised with their own pollen, though exceptions are not rare.
- (2) The chief exceptions seem to arise where the parents or the ancestors of the variety have been variable.
- (3) Slight variations are seldom hereditary.

¹ See Dr Maxwell Masters, in Veitch's *Manual of Orchids*, x. 1894, p. 45, figs. 6, 7.

² In the light of Mendelism the above facts suggest that the normal form is dominant to the peloriate form which is recessive. (*Note added 1914.*)

- (4) Abnormal sports are generally transmitted wholly or not at all.
- (5) Distinct varieties, as a general rule, transmit their qualities in different degrees, sometimes wholly, sometimes partly, and at other times not at all.
- (6) Varietal characters can seldom be traced in the second or following generations, unless they happen to recur on both sides of the pedigree.
- (7) The law of *Partial Prepotency*, elaborated later in this paper, may possibly account for these varied results in the inheritance of varietal characters.

THE INHERITANCE OF SPECIFIC CHARACTERS.

Those who have studied hybrids between distinct species must be impressed with the undoubted inheritance of specific characters.

Varietal characters, while perhaps of more practical importance, are yet so indefinable, so uncertain, and so fleeting that in the second generation they are with difficulty traced at all. On the other hand, specific characters are more definable, more certain, and more lasting, and can be traced through several generations. For instance, in *Paphiopedilum* \times *triumphans*, a hybrid of the third generation raised by M. Jules Hye-Leysen, of Ghent, the crimson veining in the upper sepal of the flower can be traced through the parent, *P.* \times *œnanthum superbum*, and the grandparent, *P.* \times *Harrisianum*, back to the great-grandparent, *P.* *barbatum*.

In studying the inheritance of specific characters, I have found it an advantage to take a special group of plants and to study their characters as carefully and minutely as a monographer would do, and in this way I have been able to follow the inheritance of specific characters more easily than otherwise I could have hoped to do. In following out this idea I have chosen the orchideous genus *Paphiopedilum* (Pfitz), better known in gardens as *Cypripedium*, partly because hybridisation has been carried farther in this genus than in many others, and partly because I have the good fortune to have a large collection of living hybrids and their parents of this genus under my own observation from day to day.

The limits of this paper will not allow fully detailed observations, but a few condensed analyses of some primary hybrid *Paphiopedilums* will serve to illustrate the inheritance of specific characters. In these cases practically the whole plant has been analysed from living specimens, twenty points in all being taken into consideration :—

(1) The habit of growth; (2) the habit of flowering; the form or shape of the (3) leaves, (4) scape, (5) bract, (6) ovary, (7) upper sepal, (8) lower sepal, (9) petals, (10) lip or slipper, (11) staminode; the colour of the (12) leaves, (13) scape, (14) bract, (15) ovary, (16) upper sepal, (17) lower sepal, (18) petals, (19) lip or slipper, (20) staminode.

Each of these parts or organs of the hybrid has been compared with the same part of each of the parent species. Each part is then classed in relation to the two parents, either (*a*) in the ratio 1:1, which represents the part as fairly intermediate between the two parents; or (*b*) in the ratio 3:2, which represents one parent to be slightly predominant in that particular part; or (*c*) in the ratio 2:1, showing the decided prepotency of one parent in that part; or (*d*) in the ratio 3:1, showing the very large prepotency of one parent in that part. In this way the twenty parts are classified, and when the various figures are added together one can see at a glance the total ratio of one parent to the other in the hybrid. In the following condensed analyses I have ignored, for the sake of simplicity, all the ratios 1:1 and also those 3:2, classing them as intermediate or thereabouts, and only showing the undoubted prepotencies of either parent in the ratios 2:1 and over. At the end of each are given the full ratios of the plant as a whole, as originally analysed, with the corresponding percentages of the predominant parent, for the sake of comparison. (For additional instances, see also under the heading of "The Variation of Primary Hybrids," p. 68.)

(1) *Paphiopedilum* × *Winnianum*, a hybrid raised by Messrs Veitch, of Chelsea out of *P. villosum* (Pfitz) (figs. 8 and 11) by *P. Druryi* (Pfitz). *In form*, the parent *P. Druryi* is prepotent in habit of growth, leaves, scape, and lower sepal; while *P. villosum* predominates in habit of flowering, petals, and staminode; in all, favouring *P. Druryi* as 18:17. *In colour*, *P. Druryi* preponderates in the leaves, lower sepal, and staminode; while *P. villosum* prevails in the petals; altogether favouring *P. Druryi* as 16:15. The whole plant in form and colour favouring *P. Druryi* as 34:32, or 51·5 per cent.

(2) *P. × Swinburnei* (fig. 67), a hybrid raised by Messrs Heath, of Cheltenham, out of *P. insigne* (Pfitz) (figs. 9, 25, 59, 62 and 74) by *P. Argus* (Pfitz). *In form*, the parent *P. insigne* is prepotent in bract, ovary, and upper sepal; while *P. Argus* predominates in the lip; in all, favouring *P. insigne* as 24:23. *In colour*, *P. Argus* predominates in lower sepal, petals, and lip, altogether favouring that parent as 19:15. The whole plant, in form and colour favouring *P. Argus* as 42:39, or 51·8 per cent.

(3) *P. × Ceres Medea*¹, a hybrid between *P. Spicerianum* (Pfitz) (fig. 6) and *P. hirsutissimum* (Pfitz), first raised by Mr Latham of Birmingham. *In form*, the parent *P. Spicerianum* is prepotent in the upper sepal, while *P. hirsutissimum* predominates in the leaves, ovary, and staminode; in all, favouring *P. hirsutissimum* as 20 : 19. *In colour*, *P. Spicerianum* preponderates in the leaves, bract, upper sepal, and staminode; while *P. hirsutissimum* prevails in the scape and petals, altogether favouring *P. hirsutissimum* as 16 : 15. The whole plant, in form and colour, favouring *P. hirsutissimum* as 36 : 34, or 51·4 per cent.

(4) *P. × Arthurianum*, a hybrid out of *P. Fairieanum* (Pfitz) by *P. insigne* (Pfitz), raised by Messrs Veitch. *In form*, the parent *P. insigne* is prepotent in the upper sepal, while *P. Fairieanum* predominates in the lip and staminode; in all, favouring *P. Fairieanum* as 23 : 20. *In colour*, *P. insigne* preponderates in the scape and upper sepal, while *P. Fairieanum* prevails in the staminode; altogether, intermediate, as 16 : 16. The whole plant, in form and colour, favouring *P. Fairieanum* as 39 : 36, or 52 per cent.

(5) *P. × concolor-villosum*, a hybrid between *P. concolor* (Pfitz) and *P. villosum* (Pfitz), raised by Messrs Charlesworth, of Bradford. *In form*, the parent *P. concolor* is prepotent in the leaves and lip, while *P. villosum* predominates in bract and ovary; in all, favouring *P. villosum* as 23 : 22. *In colour*, *P. concolor* preponderates in the lower sepal and lip, while *P. villosum* prevails in the leaves and bract; altogether favouring *P. concolor* as 15 : 12. The whole plant, in form and colour, favouring *P. concolor* as 37 : 35, or 51·3 per cent.

(6) *P. × Ashburtoniae Laforcadei* (fig. 71), a hybrid raised by M. Bauer, of Paris, out of *P. barbatum* by *P. insigne Chantinii* (fig. 9). *In form*, the parent *P. barbatum* is prepotent in habit of growth, leaves, lip, and staminode; while *P. insigne* preponderates in the lower sepal and petals; in all, favouring *P. barbatum* as 20 : 18. *In colour*, *P. insigne* predominates in the lower sepal. Altogether the hybrid is fairly intermediate, as 15 : 15. The whole plant, in form and colour, favouring *P. barbatum* as 35 : 33, or 51·4 per cent.

(7) *P. × apiculatum* (fig. 69), a hybrid raised by Mr D. V. Drewett, of Riding-Mill-on-Tyne, out of *P. barbatum* (Pfitz) by *P. Boxallii* (Pfitz) (fig. 72). *In form*, the parent *P. barbatum* is prepotent in habit of growth, leaves, and staminode, while *P. Boxallii* predominates in the petals; in all, favouring *P. barbatum* as 26 : 21. *In colour*, *P. Boxallii*

¹ Now named *C. Medeia* (fig. 68), cf. *Orchid Stud-Book*, 1909, p. 183. (Note added 1914.)

preponderates in the bract, petals, and lip, while *P. barbatum* prevails in the staminode; altogether favouring *P. Boxallii* as 19 : 15. The whole plant, in form and colour, favouring *P. barbatum* as 41 : 40, or 50·6 per cent.

(8) *P. × selligerum* (fig. 66), a hybrid out of *P. barbatum* (Pfitz) by *P. philippinense* (Pfitz), raised by Messrs Veitch. *In form*, the parent *P. barbatum* is prepotent in the leaves, while *P. philippinense* predominates in habit of flowering, ovary, and lower sepal; in all, favouring *P. philippinense* as 20 : 19. *In colour*, *P. barbatum* preponderates in the lip, while *P. philippinense* prevails in the leaves and lower sepal; altogether fairly intermediate, as 16 : 16. The whole plant, in form and colour, favouring *P. philippinense* as 36 : 35, or 50·8 per cent.

(9) *P. × Doncasterianum II.*, a hybrid between *P. hirsutissimum* (Pfitz) and *P. callosum* (Pfitz), raised by Messrs Charlesworth. *In form*, the parent *P. callosum* is prepotent in habit of flowers, scape, bract, ovary, lower sepal, and staminode, while *P. hirsutissimum* predominates in the leaves and lip; in all, favouring *P. callosum* as 24 : 20. *In colour*, *P. callosum* preponderates in scape, ovary, lower sepal, lip and staminode, while *P. hirsutissimum* prevails in leaves, bract, and petals; altogether fairly intermediate, as 15 : 15. The whole plant, in form and colour, favouring *P. callosum* as 39 : 35, or 52·7 per cent.

(10) *P. × Quies II.*, a hybrid between *P. Curtisii* and *P. Hookeræ volonteana*, raised by Messrs Charlesworth. *In form*, the parent *P. Hookeræ* is prepotent in habit of flowering, scape, and lip, while *P. Curtisii* predominates in habit of growth, bract, ovary, and petals; in all, fairly intermediate, as 19 : 19. *In colour*, *P. Hookeræ* preponderates in the ovary and upper sepal, while *P. Curtisii* prevails in the bract; altogether favouring *P. Hookeræ* as 17 : 16. The whole plant, in form and colour, favouring *P. Hookeræ*, as 36 : 35, or 50·7 per cent.

From the above analyses it will be seen that in primary hybrids between two species the amount of the inheritance of the specific characters of each parent is found to be about one-half.

THE INHERITANCE OF GENERIC CHARACTERS.

Generic hybrids, or bigeners, *i.e.* hybrids between species belonging to two distinct genera, have now become rather numerous, especially in the Orchideæ, in that order numbering about 150 distinct crosses. As a rule it is found that generic characters, like specific characters, are inherited in primary hybrids to the amount of one-half or there-

abouts. An interesting illustration of this may be seen in the structure of the pollinia in the many hybrids between *Cattleya* and *Lælia*.

The genus *Cattleya* (Lindl.) has four pollinia of equal size, arranged in one row, while *Lælia* (Lindl.) has eight pollinia of equal size, arranged in two rows of four each, being generally somewhat smaller than those of *Cattleya*.

The hybrid genus *Lælio-Cattleya* × (Rolfe), obtained by crossing these two genera, has eight pollinia, arranged in two rows of four each, as in the parent *Lælia*; but in the lower row the pollinia are large and of equal size, as in the parent *Cattleya*, while in the upper row they are small, uneven, and apparently rudimentary. In this way the generic characters of both parents are inherited.

Generic characters appear to be more powerful and more lasting than either specific or varietal characters, persisting, little changed for several generations; and would, no doubt, be much more difficult to breed out than either specific or varietal characters.

For example, *Lælio-Cattleya* × *leucoglossa*, raised by Messrs Veitch, is a hybrid of the third generation, whose pedigree may be seen at a glance in the following diagram:—

DIAGRAM SHOWING THE TWO PARENTS, FOUR GRANDPARENTS, AND EIGHT GREAT-GRANDPARENTS OF *LÆLIO-CATTLEYA* × *LEUCOGLOSSA*.

C.	C.	C.	C.	C.	C.	C.	L.
L.	L.	L.	L.	L.	L.	Mossiaë	crispa
♀	♂	♀	♂	♀	♂	♀	♂
C. L.		C. L.		C. L.		L.-C. × exoniensis	
♀		♂		♀		♂	
Cattleya				Lælio-Cattleya			
Loddigesii				× fausta			
♀				♂			

LÆLIO-CATTLEYA × *LEUCOGLOSSA*.

According to Galton's law of ancestral heredity, this hybrid should represent $\frac{1}{2}$ C. Loddigesii + $\frac{1}{4}$ L.-C. × fausta + $\frac{1}{8}$ C. Loddigesii + $\frac{1}{16}$ L.-C. × exoniensis + $\frac{1}{32}$ C. Mossiaë + $\frac{1}{32}$ L. crispa; or, to reduce it

to more simple terms, $\frac{3}{4}$ *C. Loddigesii* + $\frac{1}{8}$ *C. Mossiæ* + $\frac{1}{8}$ *L. crispa*; that is to say, $\frac{7}{8}$ *Cattleya* + $\frac{1}{8}$ *Lælia*. Yet, when we come to examine the generic characters of this complex hybrid, we find that it is a true *Lælio-Cattleya*, having eight pollinia in two rows of four each, the upper row being small and apparently rudimentary; and although the *Lælia* ancestry is only represented to the extent of $\frac{1}{8}$, yet the generic characters are the same as if it had been $\frac{1}{2}$. In other words, through its parent and grandparent the hybrid has inherited the generic characters of one of its great-grandparents, while the specific characters of that ancestor can be traced but little, and the varietal characters not at all.

Generic hybrids in the Orchideæ have produced many anomalies; for instance, when the species of *Lælia*, *Cattleya*, and *Sophronitis* are intercrossed, normal hybrids are produced, intermediate in their generic characters; but when species of *Lælia*, *Cattleya*, and *Sophronitis* are crossed with the reed-like species of *Epidendrum*, the latter genus is always prepotent to a remarkable extent, completely swamping the other genera, no matter how they may have been crossed; yet, in every case, in specific and varietal characters, one can easily trace the influence of the other parents, thus proving that the cross has been really and truly made.

Seven positive cases, and no negative ones, of these prepotent *Epidendrum* crosses are on record, and all agree in this curious generic prepotency.

(1) *Epiphronitis* × *Veitchii*, raised by Messrs Veitch out of *Sophronitis grandiflora* (Lindl.) by *Epidendrum radicans* (Pav.).

(2) *Epi-Cattleya* × *matutina* (fig. 44), raised by Messrs Veitch out of *Cattleya Bowringiana* (Veitch), by *Epidendrum radicans* (fig. 46).

(3) *Epi-Lælia* × *radico-purpurata* (fig. 45 *Veitchii*), raised both by Messrs Veitch and Messrs Charlesworth out of *Lælia purpurata* (Lindl.), by *Epidendrum radicans*.

(4) *Epi-Lælia* × *Charlesworthii*, raised by Messrs Charlesworth out of *Lælia cinnabarina* (Lindl.), by *Epidendrum radicans*.

(5) *Epi-Cattleya* × "*Mrs James O'Brien*," raised by Messrs Veitch

¹ Later observations suggest that the generic characters which distinguish *Cattleya* and *Lælia* segregate in Mendelian fashion; if so, the Mendelian expectation in this case would be 1 *Cattleya*: 1 *Lælio cattleya*. (Note added 1914.)

² Now named *E.-c. O'Brienæ*, Rolfe and Hurst, *Orchid Stud-Book*, 1909, p. 85. (Note added 1914.)

out of *Cattleya Bowringiana*, by *Epidendrum* \times *O'Brienianum* (Veitch), the latter parent being itself a hybrid out of *E. cinctum* (Hook. f.), by *E. radicans*.

(6) *Epi-Lælia* \times *heatonensis* (Charlesworth), out of *Lælia cinnabarina*, by *Epidendrum* \times *O'Brienianum*.

It is difficult to account for this anomaly, but I have suggested in another place that possibly the aristocratic *Cattleya* and *Lælia*, as well as the more modest *Sophranitis*, are all descended—or should it not be *ascended*!—from a lowly reed-like *Epidendrum* ancestor, and, when crossed with their poor relations, tend to revert to their common ancestor (see pp. 35 and 48).

In addition to these *Epidendrum* hybrids there are eleven curious crosses between very distinct genera, which, strangely enough, have all reproduced the characters of their seed-parents almost exactly.

(1) *Zygopetalum Mackayi* ♀ crossed with *Odontoglossum nobile* (Pescatorei) ♂, both by Messrs Veitch, of Chelsea, and by Messrs Heath, of Cheltenham, produced over 300 plants, of which more than twenty flowered *Z. Mackayi* pure and simple (the remainder were thrown away unflowered, but all were evidently the same species).

(2) *Zygopetalum Mackayi* ♀ crossed with *Odontoglossum crispum* ♂.

(3) *Z. Mackayi* ♀ crossed with *O. grande* ♂.

(4) *Z. Mackayi* ♀ crossed with *O. bictonense* ♂.

(5) *Z. Mackayi* ♀ crossed with *Lycaste Skinnerii*, all by Messrs Veitch, produced a few seedlings of each cross, all of which flowered pure *Z. Mackayi*.

(6) *Z. Mackayi* ♀ crossed with *Oncidium unguiculatum* ♂, by Rev. F. D. Horner, of Burton-in-Lonsdale, and by a Florentine hybridist, both produced *Z. Mackayi*, pure and simple, four plants being raised.

(7) *Epidendrum* \times *O'Brienianum* ♀ crossed with *Dendrobium crystallinum* ♂, by Mr Statter, of Stand Hall, near Manchester, produced a large number of plants, all of which flowered *E.* \times *O'Brienianum*.

(8) *Phragmipedium longifolium Hartwegii* ♀ crossed with *Paphiopedilum Stonei* ♂, by Mr R. M. Grey, for Mr Graves, of Orange, Mass., produced a plant which flowered *Phrag. longifolium Hartwegii*.

(9) *Phrag.* \times *Sedenii* ♀ crossed with *Paph. Stonei* ♂, by Mr Statter, produced a plant which flowered *Phrag.* \times *Sedenii* (as far as one could determine from a somewhat imperfect first flower). I also have an unflowered plant of the same cross, which is undoubtedly a *Phragmipedium* in its habit of growth, and form and colour of leaves.

(10) *Lælia harpophylla* ♀ crossed (curiously enough) with *Paphiopedilum villosum* ♂ (belonging to a distinct *sub-order*) and the reverse cross, viz.—

(11) *Paph. villosum* ♀ × *Lælia harpophylla* ♂, both raised by a well-known expert hybridist in the North of England, have produced plants, yet unflowered, which I have seen and examined, and which, in each case, have the habit and characteristics of their respective seed-parents, No. 10 being evidently true *Lælia* and No. 11 true *Paphiopedilum*.

Here we have eleven distinct crosses between nine very distinct genera, all of which have produced "false hybrids," reproducing the characters of their seed-parents absolutely unmodified by the so-called pollen-parents. Nor are these mere solitary exceptions, for so far as experiments have yet been made they seem to be the absolute rule with no exception; in one case, as we have seen, no less than 300 plants were raised from one capsule, all with the same result. These curious crosses are evidently very different from the prepotent *Epidendrum* hybrids, for in the latter it was the pollen-parent that was prepotent, and all of them were slightly modified by the influence of the other parent, showing them to be true hybrids. But those now under consideration are evidently not hybrids at all, showing no *trace* of one of the so-called parents.

In the face of modern knowledge concerning the germ-cells and the inner processes of reproduction, it would be idle for us to assert that the seeds which produced these plants had ever been hybridised. They must therefore have been fertilised with their own pollen, or have reproduced themselves by parthenogenesis. After a lengthy correspondence and a careful sifting of the facts, I have come to the conclusion that in eight cases at least out of the eleven, self-fertilisation is quite out of the question, being practically impossible in the circumstances¹. There seems to remain to us then one reasonable explanation, and that is parthenogenesis.

Parthenogenesis, or the production of fertile seeds in a capsule without fertilisation, is well known to occur in certain plants, *e.g.* *Gnaphalium*, *Mercurialis*, and *Cœlebogyne*².

Professor Henslow, in his *Structure of Flowers*, p. 171, relates how Dr Treub found a larva of an insect in the ovary of a Mauritian Orchid, *Liparis latifolia*, which seemed to feed on the juices secreted therein,

¹ See *Journ. Roy. Hort. Soc.* **xxi.** 1898, p. 477. (See pp. 36 and 37.)

² Kerner and Oliver, *Nat. Hist. Plts.* **II.** p. 469.

without injuring either the ovules or the ovary. In a short time, *without the aid of pollen*, the ovules developed and became covered with seed-coats, as if under the influence of pollination; the irritation of the larva seemed to have developed the ovules in the same way the pollen tubes would have done. And this is possibly what has happened with these curious crosses. The pollen tubes of the distinct genera may have irritated and developed the ovules by feeding on the juices secreted by the ovary, yet by some incompatibility failed to fertilise the egg-cells, the result being seed-buds developed within the capsule, naturally bearing the characters of the seed-parent only. [Whether these seed-buds arise direct from the egg-cells, or from the antipodal cells as in cases of polyembryony in *Fuchsia*, *Allium*, and *Citrus*, yet remains to be seen¹.] There is, however, one slight difficulty in this explanation which puzzled me for some time, and that is that hitherto it was generally understood that in parthenogenesis all the plants were exactly alike from one capsule, reproducing the varietal characters of the seed-parent down to the minutest detail, just in the same way as ordinary buds and cuttings do; whereas, in the case of the *Zygopetalum* crosses particularly, the seedlings varied in colour, form, and size, both *inter se*, and from the seed-parent also.

But recent experiments with *Daphnia* have shown that there is a certain amount of variation even in parthenogenetic offspring²; and as it has been already demonstrated that at least one nuclear division occurs in parthenogenesis³, this might reasonably have been expected. The one difficulty, therefore, in accepting parthenogenesis as the explanation of the above curious crosses seems now to be removed.

THE VARIATION OF PRIMARY HYBRIDS.

Hybrids of the first generation between the same pair of species are found to have a certain-specific likeness, yet at the same time they differ one from the other in varietal characters.

Sex, *per se*, does not seem to have any influence in the variation of hybrids in the Orchideæ (owing possibly to their being usually herm-

¹ *N. H. P.* II, p. 469.

² Roy. Soc. 4/5/99, *Nature*, 59, p. 142. Cf. also the interesting case of the segregation of the horned and hornless characters in the parthenogenetic reproduction of *Chitumnus* ("Stick Insect" of Ceylon) described by Fryer in *Journ. of Genetics*, Vol. 3, p. 108 (1913.) (*Note added 1914.*)

³ Weismann's *Germ Plasm*, 1893, p. 347.



Fig. 67. \times *P. Swinburnei* Kerch.
 Fig. 66. \times *P. selligerum* Stein. Fig. 68. \times *P. Medeia* Stein var. *Ceres* Hurst.
 Hybrid *Paphiopedilums* at Burbage.

Fig. 69.
 \times *P. apiculatum*
 Stein.

Fig. 70.
 \times *P. Lathamianum*
 Stein.

Fig. 71.
 \times *P. Ashburtoniae* Stein
 var. *Laforcadei* Hurst.



Fig. 72.
P. Boxallii
 Pfitz.

Fig. 73.
 \times *P. rubescens*
 Hurst.

Fig. 74.
P. insigne Pfitz. var.
maculatum Hurst.

From a photograph taken at Burbage.



Fig. 75. \times *Paphiopedilum Lathamianum* Stein.

A Primary Hybrid from *P. Spicerianum* Pfitz. (fig. 6) and *P. villosum* Pfitz. (fig. 8).

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aphrodite by nature¹), the same varieties occurring both in the reverse and obverse crosses; indeed, in several cases recorded, the progeny of the reverse cross and that of the original one have proved to be exactly the same. As we have seen in the inheritance of varietal characters, when a different variety is used as a parent, the result tends to be different, the variation generally corresponding with that of the variety used. But the variation of primary hybrids extends beyond the differences caused by using different varieties as parents, because we often get considerable variation among hybrids raised from the same seed-capsule (cf. fig. 24).

How then is this variation to be explained? A careful analysis of hybrids of *Paphiopedilum* seems to give a clue to this problem, as the following condensed analyses show. (Compare also those given under the heading of "The Inheritance of Specific Characters," p. 60.)

(1) (a) *Paphiopedilum* \times *Lathamianum* I (fig. 70).—A hybrid between *P. Spicerianum* (Pfitz) and *P. villosum* (Pfitz), first raised by Mr Latham, of Birmingham. *In form*, the parent *P. Spicerianum* is prepotent in the lower sepal and lip, while *P. villosum* predominates in the leaves; in all, favouring *P. Spicerianum* as 20 : 15. *In colour*, *P. Spicerianum* preponderates in the bract and upper sepal, while *P. villosum* prevails in the scape and lip; altogether favouring *P. Spicerianum* as 18 : 17. The whole hybrid, in form and colour, favouring *P. Spicerianum* as 38 : 32, or 54·2 per cent.

(1) (b) *P. \times Lathamianum* II (fig. 7).—Another variety of the same parentage. *In form*, the parent *P. Spicerianum* is prepotent in the leaves, lower sepal, and lip; in all favouring that parent as 23 : 17. *In colour*, *P. Spicerianum* predominates in the upper sepal and staminode, while the other parent, *P. villosum*, preponderates in the scape and petals, altogether favouring *P. villosum* as 17 : 15. The whole plant, in form and colour, favouring *P. Spicerianum* as 38 : 34, or 52·7 per cent.

(1) (c) *P. \times Lathamianum* III (fig. 75).—A third variety of the same parentage. *In form*, *P. Spicerianum* is prepotent in the scape, while *P. villosum* predominates in the habit of growth, ovary, lower sepal, and lip; in all favouring *P. villosum* as 21 : 18. *In colour*, *P. Spicerianum* preponderates in the scape, bract, upper sepal, and staminode; while *C. villosum* prevails in the ovary, petals, and lip; altogether fairly intermediate, as 15 : 15. The whole plant, in form and colour, favouring *P. villosum* as 36 : 33, or 52·1 per cent.

¹ The demonstration by Miss Saunders that in Stocks (*Matthiola*) the factors borne by the ovules of a plant may be different from the factors borne by the pollen-grains of the same plant, seems to dispose of this suggestion. See Report IV. *Evol. Com. Roy. Soc.* 1908, p. 39. (Note added 1914.)

(2) (a) *P. × Harrisianum I.*—A hybrid between *P. villosum* (Pfitz) and *P. barbatum* (Pfitz) first raised by Messrs Veitch. *In form*, the parent *P. villosum* is prepotent in the habit of growth and leaves, while *P. barbatum* predominates in the staminode; in all, fairly intermediate, as 16 : 16. *In colour*, *P. villosum* preponderates in the upper sepal, while *P. barbatum* prevails in the leaves, bract, and staminode; altogether favouring *P. barbatum* as 16 : 13. The whole plant, in form and colour, favouring *P. barbatum* as 32 : 29, or 52·4 per cent.

(2) (b) *P. × Harrisianum II.*—Another variety of the same parentage. *In form*, *P. villosum* is prepotent in the habit of growth, while *P. barbatum* predominates in leaves and staminode; in all, favouring *P. barbatum* as 17 : 16. *In colour*, *P. barbatum* prevails in the leaves, altogether being fairly intermediate, as 15 : 15. The whole plant, in form and colour, favouring *P. barbatum* as 32 : 31, or 50·7 per cent.

(2) (c) *P. × Harrisianum III.*—A third variety of the same parentage. *In form*, *P. barbatum* is prepotent in the habit of growth, leaves, and staminode; in all, favouring that parent as 19 : 16. *In colour*, *P. barbatum* predominates in the leaves, bract, upper sepal, and staminode; altogether favouring that parent as 17 : 12. The whole plant, in form and colour, favouring *P. barbatum* as 36 : 28, or 56·2 per cent.

(3) (a) *P. × Leeaenum giganteum.*—A hybrid out of *P. Spicerianum* (Pfitz) by *P. insigne* (Pfitz), var. *giganteum* (fig. 62), raised by Messrs Heath, of Cheltenham. *In form*, the parent *P. Spicerianum* is prepotent in the leaves and upper sepal, while *P. insigne* predominates in the petals; in all, fairly intermediate as 17 : 17. *In colour*, *P. Spicerianum* preponderates in the upper sepal and petals, altogether favouring that parent as 18 : 15. The whole plant, in form and colour, favouring *P. Spicerianum* as 35 : 32, or 52·2 per cent.

(3) (b) *P. × Leeaenum superbum* (fig. 61).—A hybrid of the same specific parentage, raised by Mr Chas. Winn, of Birmingham; but in this case *P. insigne Chantinii* was the parental variety. *In form*, *P. Spicerianum* is prepotent in the upper sepal, lower sepal, and petals, while *P. insigne* predominates in the habit of growth, leaves, lip, and staminode; in all, favouring *P. insigne* as 22 : 17. *In colour*, *P. Spicerianum* preponderates in the upper sepal, while *P. insigne* prevails in the lower sepal and staminode; altogether favouring *P. Spicerianum* as 17 : 16. The whole plant, in form and colour, favouring *P. insigne* as 38 : 34, or 52·7 per cent.

(3) (c) *P. × Leeaenum Albertianum.*—A hybrid of the same specific parentage, raised by M. Jules Hye-Leysen, of Ghent, the parental variety used being *P. insigne Wallacei*. *In form*, *P. Spicerianum* is prepotent in the habit of growth; in all, favouring that parent as 24 : 23. *In colour*,

P. Spicerianum predominates in the leaves, while *P. insigne* preponderates in the lower sepal and lip; altogether favouring *P. insigne* as 17:16. The whole plant, in form and colour, being fairly intermediate, as 40:40, or 50 per cent. of each parent.

(4) (a) *P. × nitens I* (fig. 10).—A hybrid out of *P. villosum* (Pfitz) by *P. insigne* (Pfitz), var. *Chantinii*, raised by Messrs Veitch. *In form*, the parent *P. insigne* is prepotent in the ovary and lip; in all, favouring that parent as 23:19. *In colour*, *P. insigne* predominates in the upper sepal, lower sepal, and staminode, while *P. villosum* preponderates in the leaves; altogether favouring *P. insigne* as 19:13. The whole plant, in form and colour, favouring *P. insigne* as 42:32, 56·7 per cent.

(4) (b) *P. × nitens II*.—A second variety of the same parentage, received by me from Mr Winn, of Birmingham. *In form*, *P. insigne* is prepotent in the ovary and lip; in all, favouring that parent as 23:19. *In colour*, *P. insigne* predominates in the upper sepal, lower sepal, and staminode; altogether favouring that parent as 18:12. The whole plant, in form and colour, favouring *P. insigne* as 41:31, or 56·9 per cent.

(4) (c) *P. × nitens III*.—A third variety of the same parentage, received by me from Mr Reginald Young, of Liverpool, and known as *var. giganteum*. *In form*, *P. insigne* is prepotent in the ovary and upper sepal, while *P. villosum* predominates in the habit of growth and leaves; in all, favouring *P. villosum* as 20:19. *In colour*, *P. insigne* predominates in the upper sepal and lower sepal, while *P. villosum* prevails in the ovary; altogether favouring *P. insigne* as 16:12. The whole plant, in form and colour, favouring *P. insigne* as 35:32, or 52·2 per cent.

(4) (d) *P. × nitens IV*.—A fourth variety of the same parentage, raised by Messrs Veitch, and known generally as *var. superbum*. *In form*, *P. insigne* is prepotent in habit of growth, ovary, and upper sepal; in all, favouring that parent as 25:18. *In colour*, *P. insigne* predominates in the leaves, upper sepal and staminode; altogether favouring that parent as 19:13. The whole plant, in form and colour, favouring *P. insigne* as 44:31, or 58·6 per cent.

(4) (e) *P. × nitens Sallierii*, really the typical hybrid from typical forms of both parents, and received by me from Mr Reginald Young, of Liverpool. *In form*, *P. villosum* is prepotent in the petals; in all, favouring that parent as 22:20. *In colour*, *P. insigne* predominates in the leaves, upper sepal, and lower sepal, while *P. villosum* preponderates in the petals; altogether favouring *P. insigne* as 19:15. The

whole plant, in form and colour, favouring *P. insigne* as 39 : 37, or 51·3 per cent.

These hybrids, as a whole, are fairly intermediate between their two parents, yet there is in most cases a local predominance of one parent or the other in one part or another of the hybrid. This applies equally either to form or colour.

When several hybrids from the same pair of species are compared together, this variation of the parts, or *Partial Prepotency*, as I propose to call it, becomes even more apparent and more diverse. For example, with three hybrids raised from the same parents, in the first, the pollen-parent may predominate in form in a certain part; in the second, the seed-parent may prevail in that part; while in the third, that part may be fairly intermediate between both parents; but in regard to colour, these conditions may be exactly reversed. But this only includes one part of the hybrid, and the same law applies equally to every one of the parts; so that when the changes are rung on twenty or more different parts by the two parents, in both form and colour, we can well understand the many possibilities of variation in hybrids of the same parentage; and I venture to suggest that this law of *Partial Prepotency*, founded on actual facts observed in hybrids of *Paphiopedilum*, may perhaps throw some light on the question of variation in offspring of the same parents. Yet, notwithstanding this variation in the parts, it is a remarkable fact that in primary hybrids the whole plant taken together is fairly intermediate between the two parents, the balance of power being well maintained in the whole.

The greatest extreme observed by me, out of many cases in *Paphiopedilum*, has been 58·6 per cent. of one parent, against 42·4 per cent. of the other, the great majority being approximately 50 per cent. of each parent. This hardly coincides with the popular belief that some hybrids resemble one parent, while others resemble the other; but this may be due simply to superficial observation, for where conspicuous parts lean towards one parent, the casual observer might easily be deceived, not noticing the inconspicuous parts which compensate for this by leaning towards the other parent.

THE VARIATION OF SECONDARY HYBRIDS.

Hybrids of the second generation, whether of two, three, or four species, differ notably from hybrids of the first generation of two species by reason of their much wider range of variation (cf. figs. 24—28). Whether this is due simply to the increased factors in their pedigree, or whether apart from



Fig. 76. *P. Spicerianum* Pfitz. ♀ × Fig. 77 × *P. nitens* Stein var. *Hycanum* Hurst ♂.
gave

Fig. 78. × *P. aureum* Hurst.
var. *Cyrus* Hurst.

Fig. 79. × *P. a. Hebe*
Hurst.

Fig. 80. × *P. a. Marie*
Closson Hurst.

Fig. 81. × *P. a. Ædipe*
Hurst.

Fig. 82. × *P. a. vir-*
ginale Hurst.

Fig. 83. × *P. a. Surprise*
Hurst.

Six F_2 siblings of × *Paphiopedilum aureum* Hurst with their parents.



Fig. 83a. × *Paphiopedilum aureum* var. *Surprise* Hurst.

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that, I have not yet been able to gather sufficient evidence to determine; still, the fact remains that, from whatever cause, hybrids of the second generation are far more variable than those of the first generation. As an illustration of this I will take two sets of hybrids in *Paphiopedilum*, in one of which we will consider the colour of the flowers, and in the other the habit, form, and colour of the leaves. Both groups are hybrids of the second generation, from three distinct species (*i.e.* a hybrid of two species crossed with a third species), and in both the law of *Partial Prepotency* is remarkably evident. The first of the two sets was raised by M. Jules Hye-Leysen, of Ghent, between varieties of *P. Spicerianum* (Pfitz) (fig. 76) and *P. × nitens* (fig. 77), the latter parent being itself a hybrid between *P. insigne* (Pfitz) and *P. villosum* (Pfitz) (*cf.* figs. 9—11). Some twenty-two hybrids have already flowered, many of them having been raised out of the same seed-capsule. Each of these hybrids has received a distinct name, and perhaps worthily so, from their wide variation and distinctness; but for the sake of convenience I will allude to them as varieties of the original one, *viz.* *P. × aureum* (figs. 78—83). The following diagram will show their pedigree at a glance:—

DIAGRAM SHOWING THE TWO PARENTS AND FOUR GRANDPARENTS
OF *PAPHIOPEDILUM × AUREUM* (vars.).

P. S.	P. S.	P. insigne	P. villosum
P. Spicerianum		P. × nitens	

PAPHIOPEDILUM × AUREUM (vars.).

According to the Galtonian law of Ancestral Heredity, these varieties should *on the average*, show $\frac{1}{2}$ *P. Spicerianum* + $\frac{1}{4}$ *P. × nitens* + $\frac{1}{8}$ *P. insigne* + $\frac{1}{8}$ *P. villosum*; or to put it more simply, $\frac{1}{2}$ *P. Spicerianum* + $\frac{1}{4}$ *P. insigne* + $\frac{1}{4}$ *P. villosum*.

The following facts will show how, in regard to the colours of the different parts of the flowers, the Galtonian law seems to be disturbed by *Partial Prepotency*:—

Colour of Flowers (comprising Upper Sepal, Lower Sepal, Petals, Lip, and Staminode).

(1) *P. × aureum*.—The parent *P. Spicerianum* is prepotent in the staminode, while the grandparent *P. insigne* predominates in the upper and lower sepals.

(2) *P. × a. Hebe*.—The parent *P. Spicerianum* and the grandparent *P. insigne* together predominate in all parts of the flower, viz. upper sepal, lower sepal, petals, lip, and staminode; indeed this variety might, at first sight, pass as a form of *P. × Leeatum* (*P. Spicerianum* × *P. insigne*), but a careful examination reveals the influence of *P. villosum*, especially in the shape and general habit of the flower (fig. 79).

(3) *P. × a. Surprise*.—The whole flower in colour resembles a greenish form of *P. insigne* *Sanderæ*, the spots of *P. insigne* and the ruby band of *P. Spicerianum* being quite obliterated in the upper sepal; yet, in form and a few minor details, its full parentage may be traced (figs. 83 and 83A).

(4) *P. × a. virginale*.—The parent *P. Spicerianum* predominates in the upper sepal and staminode, while *P. villosum* preponderates in the petals and lip. This variety would almost pass for a compact form of *P. × Lathanianum* (*P. Spicerianum* × *P. villosum*), but differs again in minor details, confirming its parentage (fig. 82).

(5) *P. × a. Augusta*.—The parent *P. Spicerianum* and the grandparent *P. insigne* together predominate in the upper sepal, while *P. Spicerianum* alone preponderates in the staminode.

(6) *P. × a. Eteocle*.—The parent *P. Spicerianum* predominates in the upper sepal, the grandparent *P. villosum* in the petals, while *P. Spicerianum* and *P. insigne* together preponderate in the staminode.

(7) *P. × a. Hermione*.—The parent *P. Spicerianum* predominates in the upper sepal, *P. insigne* and *P. villosum* together preponderate in the petals, while *P. Spicerianum* and *P. insigne* prevail in the staminode.

(8) *P. × a. Hermode*.—The parent *P. Spicerianum* and the grandparent *P. insigne* together predominate in the upper sepal, lower sepal and staminode.

(9) *P. × a. Hero*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal and staminode; while *P. Spicerianum* and *P. villosum* preponderate in the petals.

(10) *P. × a. Minos*.—*P. Spicerianum* and *P. insigne* together predominate in the staminode, *P. insigne* alone preponderates in the upper and lower sepals, and *P. villosum* alone in the petals.

(11) *P. × a. Œdipe*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal and staminode, while *P. villosum* and *P. insigne* prevail in the petals (fig. 81).

(12) *P. × a. Olympia*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal and staminode, while *P. insigne* alone prevails in the petals.

(13) *P. × a. Osiris*.—*P. Spicerianum* predominates in the upper and lower sepals; *P. villosum* alone preponderates in the petals, and *P. insigne* alone in the staminode.

(14) *P. × a. Polynice*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal, *P. insigne* and *P. villosum* in the lower sepal, and *P. Spicerianum* alone in the staminode.

(15) *P. × a. Pomone*.—*P. insigne* predominates alone in the upper sepal, *P. insigne* and *P. villosum* together in the petals, and *P. Spicerianum* and *P. villosum* in the staminode.

(16) *P. × a. Vertunne*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal and staminode, while *P. villosum* alone prevails in the petals.

(17) *P. × a. amœna*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal, *P. insigne* alone in the lower sepal, and *P. Spicerianum* alone in the petals and staminode.

(18) *P. × a. Cyrus*.—*P. insigne* and *P. Spicerianum* predominate in the upper sepal; *P. insigne* and *P. villosum* together preponderate in the petals; and *P. Spicerianum* and *P. villosum* prevail in the staminode (fig. 78).

(19) *P. × a. delicatulum*.—*P. Spicerianum* alone predominates in the upper sepal; *P. insigne* and *P. villosum* together preponderate in the petals; and *P. Spicerianum* and *P. insigne* together prevail in the staminode.

(20) *P. × a. Mellona*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal and staminode; *P. insigne* alone preponderates in the lower sepal; while *P. insigne* and *P. villosum* together prevail in the petals.

(21) *P. × a. Micias*.—*P. insigne* alone predominates in the upper sepal; while *P. insigne* and *P. villosum* together preponderate in the petals, and *P. Spicerianum* and *P. villosum* together in the staminode.

(22) *P. × a. tigrinum*.—*P. Spicerianum* and *P. insigne* together predominate in the upper sepal; *P. insigne* alone preponderates in the lower sepal; *P. Spicerianum* alone in the petals; while *P. Spicerianum* and *P. villosum* together prevail in the staminode.

Apart from the above prepotencies the parts of these twenty-two hybrids are fairly intermediate in colour between the three ancestral species.

The second set of hybrids to illustrate the variability of secondary hybrids and the law of *Partial Prepotency* consist of twenty-four plants, all raised from the same seed-capsule by Mr Reginald Young, of Liverpool, out of *P. Boxallii* (Pfitz), var. *atratum*, by *P. × politum*, the latter being itself a hybrid between *P. barbatum* and *P. venustum* (figs. 84—89.) For the sake of convenience I will class these unflowered hybrids as forms of what I believe to be the original hybrid of the same parentage, viz. *P. × Pluto*, raised by Messrs Low, of Bush Hill Park, using Roman numerals from I to XXIV to distinguish the individual varieties (fig. 90).

The following diagram will show the pedigree at a glance:—

DIAGRAM SHOWING THE TWO PARENTS AND FOUR GRANDPARENTS OF
PAPHIOPEDILUM × PLUTO (vars.).

P. B. ♂	P. B. ♀	P. barbatum	P. venustum
P. Boxalli atratum ♂		P. × politum ♀	

PAPHIOPEDILUM × PLUTO (vars.).

According to the Galtonian law, these varieties of the hybrid *P. × Pluto* should show, on the average, $\frac{1}{2}$ *P. Boxallii* + $\frac{1}{4}$ *P. × politum* + $\frac{1}{8}$ *P. barbatum* + $\frac{1}{8}$ *P. venustum*; or to put it more simply, $\frac{1}{2}$ *P. Boxallii* + $\frac{1}{4}$ *P. barbatum* + $\frac{1}{4}$ *P. venustum*.

The following facts will show the disturbing factor of *Partial Prepotency* in regard to the habit, form, and colour of the leaves.

Prepotencies in Habit, Form, and Colour of Leaves.

P. × Pluto, I.—The parent *P. Boxallii* is prepotent in habit and form, while the grandparent *P. venustum* predominates in colour of leaves.



Fig. 86. *P. barbatum* Pfitz.

Figs. 84 and 85. *P. Boxallii* Pfitz. var. *atratum* Hurst. Fig. 87. *P. venustum* Pfitz.

Fig. 88. *P. Boxallii* Pfitz. var. *atratum* Hurst. Fig. 89. \times *P. politum* Hurst.

(The two parents and four grandparents of \times *P. Pluto* Kerch., vars. I to XXIV.)



Fig. 90. \times *Paphiopedilum Pluto* Kerch., vars. I to XXIV.

P. × Pluto, II.—The grandparent *P. venustum* predominates in colour of leaves.

P. × Pluto, III.—*P. Boxallii* alone predominates in habit, while *P. Boxallii* and *P. venustum* together preponderate in colour of leaves.

P. × Pluto, IV.—*P. Boxallii* alone predominates in habit, while *P. Boxallii* and *P. barbatum* together preponderate in colour of leaves.

P. × Pluto, V.—*P. Boxallii* predominates in form, while *P. venustum* preponderates in habit and colour of leaves.

P. × Pluto, VI.—*P. Boxallii* predominates in habit, while *P. venustum* preponderates in colour of leaves.

P. × Pluto, VII.—*P. Boxallii* predominates in habit and colour, while *P. barbatum* prevails in form of leaves.

P. × Pluto, VIII.—*P. Boxallii* alone predominates in habit and form, while *P. barbatum* and *P. venustum* together preponderate in colour of leaves.

P. × Pluto, IX.—*P. Boxallii* and *P. venustum* together predominate in habit, while *P. Boxallii* and *P. barbatum* together preponderate in colour of leaves.

P. × Pluto, X.—*P. Boxallii* and *P. venustum* together predominate in habit, while *P. Boxallii* and *P. barbatum* together preponderate in form of leaves.

P. × Pluto, XI.—The grandparent *P. barbatum* alone predominates in form, while the grandparents *P. barbatum* and *P. venustum* together preponderate in colour of leaves.

P. × Pluto, XII.—*P. Boxallii* alone predominates in habit and form, while *P. Boxallii* and *P. venustum* together preponderate in colour of leaves.

P. × Pluto, XIII.—*P. barbatum* alone predominates in form, *P. venustum* in habit, while *P. Boxallii* and *P. venustum* together prevail in colour of leaves.

P. × Pluto, XIV.—*P. Boxallii* and *P. barbatum* together predominate in habit, form, and colour of leaves.

P. × Pluto, XV.—*P. Boxallii* and *P. barbatum* together predominate in habit and colour, while *P. Boxallii* and *P. venustum* together preponderate in form of leaves.

P. × Pluto, XVI.—*P. barbatum* alone predominates in habit, while *P. Boxallii* and *P. barbatum* together preponderate in form and colour of leaves.

P. × Pluto, XVII.—*P. Boxallii* alone predominates in habit; *P. Boxallii* and *P. barbatum* together preponderate in form; and *P. Boxallii* and *P. venustum* together prevail in colour of leaves.

P. × Pluto, XVIII.—*P. venustum* alone predominates in habit; *P. barbatum* alone preponderates in form; while *P. Boxallii* and *P. venustum* together prevail in colour of leaves.

P. × Pluto, XIX.—*P. barbatum* alone predominates in habit, while *P. Boxallii* and *P. barbatum* together preponderate in form and colour of leaves.

P. × Pluto, XX.—*P. Boxallii* and *P. venustum* together predominate in habit and form of leaves.

P. × Pluto, XXI.—*P. Boxallii* and *P. barbatum* together predominate in habit, while *P. Boxallii* alone prevails in form and colour of leaves.

P. × Pluto, XXII.—*P. barbatum* alone predominates in habit and form, while *P. Boxallii* and *P. barbatum* together preponderate in colour of leaves.

P. × Pluto, XXIII.—*P. Boxallii* and *P. venustum* together predominate in habit; *P. barbatum* alone preponderates in form; and *P. Boxallii* alone in colour of leaves.

P. × Pluto, XXIV.—*P. venustum* alone predominates in habit; *P. barbatum* alone preponderates in form; while *P. barbatum* and *P. venustum* together prevail in colour of leaves.

All the hybrids, without exception, show distinct traces of both the parental and ancestral species, but in different proportions. Certain individual parts of some of the hybrids are fairly well balanced between their three pedigree species; in some parts one or other of the three species clearly predominates; while in some parts, any two of the three species prevail; and so on through all the variations, the changes being rung on the different parts by the three pedigree species, both in form and colour, giving rise to numerous variations. Indeed, in the one case detailed above, out of twenty-four hybrids raised from the same seed-capsule, no two are alike, and yet all show distinct traces of their ancestry, and well illustrate the law of *Partial Prepotency*¹.

One point may be noted here that comes out clearly in an examination of the above hybrids, and that is the latency of certain characters in the first generation which come out markedly in the second generation, *e.g.* the hybrid parent of these twenty-four hybrids, *P. × politum*,

¹ These two cases of the variation of the secondary hybrids *P. × aureum* and *P. × Pluto* are probably instances of Mendelian segregation and recombinations of the grandparental characters in the hybrids. The so-called 'law of *Partial Prepotency*', noted in this paper about a year before Mendel's paper was rediscovered, is largely an obscure anticipation of Mendelian dominance and segregation of unit-characters. (*Note added 1914.*)

fails to show the colour characters of one of its own parents, *P. barbatum*, in the leaves; yet in a number of cases these same colour characters reappear strongly in the second generation, clearly showing that certain characters may remain latent in one generation to reappear in the next¹.

THE FERTILITY OF HYBRIDS.

The question of the fertility of hybrids is very important both to the student and to the practical breeder. If a hybrid, *i.e.* a first cross between two distinct species, is not fertile, its further improvement by crossing is obviously barred; but if it is fertile in however small a degree, then in the hands of the skilled hybridist it may prove to be the starting-point of a series of variations of great economic value.

Amid the many misconceptions concerning hybrids in the popular mind perhaps none has clung so tenaciously as the belief in their absolute infertility. In studying the records of our foremost hybridists—Kolreiter, Gartner, Herbert, Darwin, Kerner, Naudin, and Focke—one is impressed at once with the undoubted fertility of many hybrids, and I have compiled a list of genera from these authorities, and from my own observations, in which fertile hybrids are known. I find that no less than ninety distinct genera are recorded in which fertile hybrids are known, and only four in which the hybrids are all quite infertile.

This list is doubtless incomplete, yet it may possibly serve a useful purpose in demonstrating the undoubted fertility of many hybrids, and the rare absolute infertility of others.

In the natural order *Compositæ* we have fertile hybrids in *Cirsium*, *Inula*, *Chrysanthemum*, *Senecio*, *Hieracium*, *Lactuca*, and *Tragopogon*.

In *Rosaceæ* we have *Prunus*, *Pyrus*, *Fragaria*, *Geum*, *Rosa*, *Rubus*, and *Cratægus*.

In *Ranunculaceæ*: *Anemone*, *Aquilegia*, and *Clematis*.

In *Gesneraceæ*: *Achimenes*, *Streptocarpus*, *Isoloma*, and *Gloxinia*.

In *Carophyllæ*: *Silene*, *Lychnis*, *Melandrium*, and *Dianthus*.

In *Liliaceæ*: *Scilla*, *Chionodoxa*, and *Chionoscilla*.

In *Solanaceæ*: *Solanum*, *Datura*, *Nicotiana*, and *Petunia*.

In *Scrophularinæ*: *Calceolaria*, *Veronica*, *Verbascum*, and *Linaria*.

In *Amarylloidæ*: *Hippeastrum*, *Crinum*, *Narcissus*.

¹ The fact that the leaf-colour of *P. barbatum* behaves as a recessive character to that of *P. venustum* is interesting, and is no doubt due to the dominance of the purple sap-colour of *P. venustum*. The absence of this dominant colour in 10 individuals of *P. × Pluto* out of the 24 analysed is not far from the Mendelian expectation of 12. (*Note added 1914.*)

In Campanulaceæ: Campanula and Lobelia.

In Geraniaceæ: Pelargonium and Ciconium.

In Ericaceæ: Rhododendron and Erica.

In Cucurbitaceæ: Cucumis and Cucurbita.

In Onagrarieæ: Enothera and Epilobium.

In Gramineæ: Triticum and Ægilops.

In Leguminosæ: Cytisus, Medicago, Pisum, and Phaseolus.

In Malvaceæ: Abutilon and Lavatera.

In Orchideæ: Paphiopedilum, Phragmipedium, Calanthe, Cattleya, Dendrobium, Disa, Epidendrum, Lælia, Lælio-Cattleya, Masdevallia, Phalænopsis, Odontoglossum, Thunia, and Chysis.

While in other natural orders we have fertile hybrids in Cotyledon, Begonia, Quercus, Gladiolus, Vitis, Cereus, Viola, Canna, Brassica, Nymphaea, Primula, Lamium, Æsculus, Berberis, Mirabilis, Salix, Mentha, Passiflora, and Fuchsia.

On the other hand, we have those genera whose hybrids, so far as experiments have yet been made, are all absolutely infertile. After a careful search I have only been able to find four of these—namely, Ribes, Polemonium, Digitalis, and Papaver—and in none of these have many experiments been made.

To my mind, negative results, though useful in their way, are never safe guides to follow. I have observed many cases in the Orchideæ where again and again certain species have refused to cross, yet at another time, and under other conditions, quite unexpectedly have produced fertile seeds; and I think that one may reasonably expect even these four recalcitrant genera to produce fertile hybrids in the course of time¹.

In regard to the ninety genera which have produced fertile hybrids, it may possibly be argued that many of them are not true hybrids, because they have been raised from closely related species; but even if this be granted, there are numerous fertile hybrids from very distinct species. For instance, the species of Lælia (Lindl.) and Cattleya (Lindl.) respectively are still classed as distinct *genera* by our best botanists; and I think that the most easy-going systematist would admit them to be distinct *species*, yet hybrids raised between these two genera are very fertile.

But perhaps the best practical proof of the fertility of hybrids is the

¹ Since the above paper was written, M. Philippe de Vilmorin, of Paris, tells us that he has succeeded in obtaining fertile hybrids in Papaver.

numerous hybrids raised in gardens, of many generations, from several species.

(1) For instance, fertile hybrids have been raised by Messrs Sutton & Sons, of Reading, between *Solanum tuberosum* and *S. Maglia*, forty-one seedlings being raised from two hybrid plants of the first generation.

(2) *Cytisus* × *præcox*, a hybrid between *C. albus* and *C. purgans*, seeds freely in my garden, and many plants have been raised in nurseries; these are the second generation of two species.

(3) As mentioned in another part of this paper, I have raised 500 plants from seeds of *Berberis* × *stenophylla*, itself a hybrid between the two species *B. Darwinii* and *B. empetrifolia*.

(4) Mr James has raised a large batch of seedlings from five hybrid *Senecios*, themselves the product of *S. cruentus* and *S. Heritieri*.

(5) *Scilla bifolia* and *Chionodoxa Lucilliae* cross naturally in gardens, and their hybrids, *Chionoscilla* × *Alleni*, seed very freely.

(6) Some of the best forms of *Narcissus* in gardens are the result of hybrids between *N. poeticus* and *N. obvallaris*, recrossed with one or other of the parent species.

(7) Our fine garden Strawberries of the present day have been raised from many generations, of two species at least, viz. *Fragaria virginiana* and *F. chilensis*, and probably in some cases, such as the variety 'St Joseph,' from *F. vesca alpina*.

(8) Hybrids between *Aquilegia californica* and *A. chrysantha*, and *A. carulea* and *A. chrysantha* crossed *inter se*, by Mr James Douglas, yielded an extraordinary variety of forms, being several generations of three species.

(9) The new race of *Streptocarpus*, raised at Kew, are from the intercrossing of hybrids between the three species, *S. Dunni*, *S. Rexi*, and *S. parviflorus*.

(10) Our garden Roses are the product of the hybridisation through many generations of at least three species, viz. *R. gallica*, *R. indica*, and *R. multiflora*; while Lord Penzance has raised hybrids between *R. lutea* and *R. rubiginosa* which are fertile, both self-crossed, and also with the race of Hybrid Perpetuals, raised originally from *R. gallica* and *R. indica*. Here we have hybrids of four distinct species.

(11) The *Amaryllis* or *Hippeastrum* of gardens have been derived from hybrids of many generations, of several species.

(12) *Gladiolus* × *Nanceianus* is a hybrid of the third generation, uniting the four species *G. psittacinus*, *G. oppositiflorus*, *G. Saundersi*, and *G. purpurato-auratus*.

(13) 'The Orchid-flowering Cannas 'Italia,' 'Austria,' 'Burbank,' &c., are the third generation of four species, namely *C. iridiflora*, *C. Warscewiczii*, *C. glauca*, and *C. flaccida*.

(14) In *Paphiopedilum* (Pfitz) (known in gardens as *Cypripedium*), twenty-eight hybrids have been recorded, each combining in its pedigree four distinct species¹.

(15) *Rhododendron* 'Eos,' raised by Mr Heale, for Messrs Veitch, of Chelsea, is a hybrid of the fourth generation, of four distinct species, viz. *R. javanicum*, *R. jasminiflorum*, *R. Lobbii*, and *R. Malayanum*; while *R. 'Numa,'* raised by the same firm, is a hybrid of the fifth generation, and contains in its pedigree the five following species:—*R. javanicum*, *R. jasminiflorum*, *R. Brookianum* *racile*, *R. indicum* (*Azalea indica* *Stella*), and *R. multicolor* *Curtisii*.

But there is another phase of the question, which is of some importance, and that is the diminished fertility of some hybrids as compared with the fertility of natural species, and it is here probably that the popular idea of the infertility of hybrids first arose. Darwin, who made a most elaborate survey of the whole question, used the word "sterility," not in the general sense of barrenness, *i.e.* absolute infertility, but rather in the sense of diminished fertility, standing as it were midway between complete fertility and absolute infertility; so that when he wrote of the "sterility of hybrids," he simply meant their lessened fertility, and not their infertility as most people seemed to imagine. Darwin, after careful research and many experiments, came to the following conclusion upon the whole matter, that "the sterility of distinct species when first united, and that of their hybrid offspring, graduates by an almost infinite number of steps from zero (when the ovule is never impregnated and a seed-capsule is never formed) up to complete fertility²." This general statement is as true to-day as it was then. Darwin then goes on to say that "...this high degree of fertility is, however, rare." Recent experiments have demonstrated that in plants this high degree of fertility is no longer rare, so that Darwin's sentence, "this high degree of fertility is, however, rare," might now read, "this high degree of sterility is, however, rare so far as plants are concerned."

Some statistics I prepared some time ago³, and now made up to 1899, serve as an illustration of this from the Orchideæ. During the past seven years Mr Reginald Young, of Liverpool, the well-known

¹ *Orch. Rev.* II. p. 361 (1894).

² *Animals and Plants*, 2nd ed. II. p. 163.

³ *Journ. Roy. Hort. Soc.* XXI. [April, 1898], p. 485 (see p. 43).

orchidist, has been crossing *inter se* some 30 distinct species and 53 distinct hybrids in the genus *Paphiopedilum* (Pfitz), and has kindly placed his stud book at my disposal, in which are precisely and carefully recorded no less than 849 crosses. Of these, taken together, 80.2% have proved fertile, *i.e.* produced good seeds. Of 263 crosses between distinct species 95.0% were fertile. This seems to show that in this genus crosses between distinct species are almost, if not quite, as fertile as crosses between varieties of the same species (taking the latter at complete fertility, *i.e.* 100%); while in crosses in which a hybrid was concerned in the parentage, out of 586, only 73.5% proved fertile, showing that crosses with hybrids, though fertile to a high degree, are yet rather less fertile than crosses between species.

A further analysis of the figures shows that while hybrids crossed with the pollen of pure species give 91.8% fertile, yet pure species crossed with the pollen of hybrids give but 60% fertile. This seems to point to the conclusion that the slight decline in the fertility of hybrids is due in a large measure to the loss of power in the pollen of hybrids (*cf.* p. 43).

This decline of power in the male element of hybrids is very curious, but has been observed before in other plants by Darwin, Dr Focke, Dr Maxwell Masters, and Prof. Macfarlane, and also by Prof. Ewart in his Zebra hybrids. Practical breeders will therefore be wise, in crossing hybrids with species, to use the pollen of species in preference to that of hybrids.

It is quite possible that domestication or cultivation may in time eradicate this decline in the fertility of hybrids, for I observe that in my hybrid *Berberis* × *stenophylla*, the first hybrids between the two wild species flower more profusely, but bear fewer berries than the parent species; while the hybrids of the second generation are much more profuse in their berry-bearing, being apparently more fruitful even than the wild species. It often happens that the pollen of very young hybrids is not so effective as that of those of more mature growth. Mr Reginald Young believes this to be so with his *Paphiopedilums*; and Dr Focke records a case of a hybrid *Sinningia* in which the pollen of the second year of flowering was better than that of the first. The decline of fertility is by no means confined to hybrids alone; for instance, certain races of *Primula sinensis* raised by Messrs Sutton, of Reading, have proved difficult to perpetuate owing to their diminished fertility, and these are cross-breds, not hybrids, being raised within the limits of one species.

In the face of these facts, therefore, we must conclude that fertility depends more upon the conditions of life than upon hybridism, and there is no reason why hybrids should not in later generations become as fully fertile as cross-breeds usually are¹.

THE STABILITY OF HYBRIDS.

Next to the question of the fertility of hybrids, perhaps the most important to the practical breeder is the constancy or stability of hybrids fertilised with their own pollen. If, as is generally supposed, hybrids do not breed true to themselves, but are inconstant and tend to revert to their grandparent species, then is the breeder's work vain, and the economic importance of hybrids considerably diminished. With a view to ascertain more precise facts than are at present on record in regard to this question, I have carried out some experiments in the genus *Berberis*, raising a large batch of *B. × stenophylla* from self-fertilised seed.

Berberis × stenophylla is a primary hybrid between *B. Darwinii* and *B. empetrifolia*, originally raised by Messrs Fisher & Holmes, of Handsworth, Sheffield.

The two parent species are very distinct. The one (*B. Darwinii*) has a vigorous and *upright* habit of growth, while the other (*B. empetrifolia*) is weak and *drooping* in habit. In the one the stems are thick, much branched, and covered with *short, woolly, brown hairs*; while the other has slender stems, little branched, and *quite glabrous*. In the one the spines are usually *seven* in number—short, spreading, and flat—while in the other they are *three (one long and two short)*, set like an inverted *T*, each rounded and grooved below. In the one the leaves number three to four, broad, flat; with five to seven spiny teeth, shiny green above, lighter below; while in the other the leaves are seven to nine, linear, closely revolute, erect, sharply mucronate, dull, dark green above, silvery below. In the one the flowers are racemose, six to twelve, orange-yellow, shaded with red without, pedicels rich red, flower segments long and narrow; while in the other, the flowers are single or sub-umbellate golden yellow, on slender green pedicels, segments short and broad.

The hybrid *B. × stenophylla* is intermediate in most characters between the two parent species. Its habit of growth is very vigorous, first upright and then drooping gracefully; stems medium thickness, branches long, pendent, slightly pubescent, with usually three spines of

¹ Recent results suggest that in certain cases both sterility and fertility may be inherited as Mendelian characters. (*Note added 1915.*)

equal size. Leaves variable, four to nine, narrow, partly revolute, sub-erect, mucronate, dark green above, silvery green below. Flowers, sub-umbellate, one to six, deep yellow, pedicels reddish, segments intermediate. Altogether the hybrid is fairly intermediate, though *B. empetrifolia* is prepotent in the number and habit of the spines; in all, favouring that parent as 13 : 12, or 52 per cent. Five hundred seedlings of this hybrid were raised, and of these no less than 90 per cent. reproduced the characters of the parent hybrid faithfully and well, with little variation¹; while the remaining 10 per cent. varied from a form representing about 66 per cent. of the grandparent *B. empetrifolia*, through a series of intermediate forms up to an extreme one, which reproduced about 67 per cent. of the characters of the grandparent *B. Darwinii*. It is worthy of notice that not one plant out of the 500 *completely* reverted to either of the ancestral species, No. 18 being the nearest to *B. Darwinii*, and No. 1 the nearest to *B. empetrifolia*.

The following condensed analysis of thirty of the most variable of these secondary hybrids will show at a glance how they differ from one another, and how far they seem to have reverted towards their grandparents. Indirectly, too, they serve to illustrate once more the law of *Partial Prepotency*.

Berberis × stenophylla vars. 1 to 30.

h = habit, f = form, c = colour.

(1) *B. empetrifolia* is prepotent in h and f of stems, h, f, and c of spines, in h, f, and c of leaves, and in h, f, and c of flowers. In all favouring that ancestor as 23 : 12, or 65·7 per cent. This form is the nearest reversion to *B. empetrifolia* in the whole batch, but traces of *B. Darwinii* still remain in all the parts, especially in the colour of the stems.

(2) *B. empetrifolia* is prepotent in h and f of stems, in h of spines, in h, f, and c of leaves, and in h of flowers. Altogether favouring that ancestor as 19 : 12, or 61·2 per cent.

(3) *B. empetrifolia* is prepotent in h, f, and c of stems, in h of spines, and in c of leaves; in all, favouring that ancestor as 17 : 12, or 58·6 per cent.

(4) *B. Darwinii* is prepotent in h, f, and c of stems, in h, f, and c of spines, in f of leaves, and in h, f, and c of flowers; altogether favouring that ancestor as 22 : 12, or 64·7 per cent.

¹ Later results with more than 3000 F_2 seedlings show that very few are precisely like the F_1 hybrid in the minor characters though a large proportion agree with the F_1 hybrid in the major characters. (*Note added 1914.*)

(5) *B. Darwinii* is prepotent in c of stems, and in h, f, and c of flowers, while *B. empetrifolia* predominates in h of spines and in h and c of leaves; in all, favouring *B. Darwinii* as 16 : 15, or 51·6 per cent.

(6) *B. empetrifolia* is prepotent in h, f, and c of stems, in h and c of spines, and in h, f, and c of leaves: altogether favouring that ancestor as 20 : 12, or 62·5 per cent.

(7) *B. Darwinii* is prepotent in f and c of stems, in f and c of leaves, and in h, f, and c of flowers, while *B. empetrifolia* predominates in h of leaves; in all, favouring *B. Darwinii* as 19 : 13, or 59·3 per cent.

(8) *B. empetrifolia* is prepotent in f and c of stems, in h and c of spines, in h, f, and c of leaves, and in h and f of flowers, while *B. Darwinii* predominates in c of flowers; in all, favouring *B. empetrifolia* as 21 : 13, or 61·7 per cent.

(9) *B. empetrifolia* is prepotent in f of stems, in h and c of spines, in h, f, and c of leaves, and in h of flowers, while *B. Darwinii* predominates in f and c of flowers; in all, favouring *B. empetrifolia* as 19 : 14, or 57·5 per cent.

(10) *B. Darwinii* is prepotent in f of stems, in f of leaves, and in f and c of flowers, while *B. empetrifolia* predominates in c of leaves; in all, favouring *B. Darwinii* as 16 : 13, or 55·1 per cent.

(11) *B. empetrifolia* is prepotent in h of stems, in h, f, and c of spines, and in f of leaves, while *B. Darwinii* predominates in f of stems, in c of leaves, and in h of flowers; in all, favouring *B. empetrifolia* as 17 : 15, or 53·1 per cent.

(12) *B. empetrifolia* is prepotent in f of stems, in h and c of spines, in f and c of leaves, and in h of flowers, while *B. Darwinii* predominates in h of leaves; in all, favouring *B. empetrifolia* as 18 : 13, or 58·0 per cent.

(13) *B. empetrifolia* is prepotent in h, f, and c of spines, in h, f, and c of leaves, and in h and f of flowers; altogether favouring that ancestor as 20 : 12, or 62·5 per cent.

(14) *B. empetrifolia* is prepotent in h of spines and in h, f, and c of leaves, while *B. Darwinii* predominates in f and c of flowers; in all, favouring *B. empetrifolia* as 16 : 14, or 53·3 per cent.

(15) *B. Darwinii* is prepotent in f and c of spines and in h, f, and c of leaves, while *B. empetrifolia* predominates in f and c of stems and in f of flowers; in all, favouring *B. Darwinii* as 17 : 15, or 53·1 per cent.

(16) *B. empetrifolia* is prepotent in h and f of stems, in c of spines, and in f and c of leaves, while *B. Darwinii* predominates in f of spines, in h of leaves, and in f and c of flowers; in all, favouring *B. empetrifolia* as 17 : 16, or 51·5 per cent.

(17) *B. Darwinii* is prepotent in f and c of stems, in f of spines, in h and f of leaves, and in h and c of flowers, while *B. empetrifolia* predominates in h of spines, in c of leaves, and in f of flowers; in all, favouring *B. Darwinii* as 19 : 15, or 55·8 per cent.

(18) *B. Darwinii* is prepotent all round in h, f, and c of stems, spines, leaves, and flowers, yet distinct traces of *B. empetrifolia* are to be found in all the parts. This form is the nearest reversion to the grandparent *B. Darwinii* in the whole batch, favouring that ancestor as 24 : 12, or 66·6 per cent.

(19) *B. Darwinii* is prepotent in h, f, and c of stems, in h, f, and c of spines, in f and c of leaves, and in h and c of flowers, while *B. empetrifolia* predominates in h of leaves and in f of flowers; in all, favouring *B. Darwinii* as 22 : 14, or 61·1 per cent.

(20) *B. empetrifolia* is prepotent in c of stems, in h of spines, and in h, f, and c of leaves; altogether favouring that ancestor as 17 : 12, or 58·6 per cent.

(21) *B. empetrifolia* is prepotent in f of stems, in h, f, and c of spines, in h, f, and c of leaves, and in h of flowers; altogether favouring that ancestor as 20 : 12, or 62·5 per cent.

(22) *B. empetrifolia* is prepotent in h and f of stems, in h of spines, in h, f, and c of leaves, and in h of flowers, while *B. Darwinii* predominates in c of stems; in all, favouring *B. empetrifolia* as 19 : 13, or 59·3 per cent.

(23) *B. Darwinii* is prepotent in c of stems and in f of leaves; while *B. empetrifolia* predominates in h of spines and c of leaves; altogether fairly intermediate (though very different at first sight from the typical hybrid) as 14 : 14, or 50 per cent.

(24) *B. empetrifolia* is prepotent in h, f, and c of spines and in h, f, and c of leaves; altogether favouring that ancestor as 18 : 12, or 60 per cent.

(25) *B. empetrifolia* is prepotent in f of stems, in h of spines, and in h and c of leaves, while *B. Darwinii* predominates in h of flowers; in all, favouring *B. empetrifolia* as 15 : 13, or 53·5 per cent.

(26) *B. empetrifolia* is prepotent in h and c of stems, in h, f, and c of spines, in f and c of leaves, and in h of flowers; altogether favouring that ancestor as 20 : 12, or 62·5 per cent.

(27) *B. Darwinii* is prepotent in c of stems, in h, f, and c of leaves, and in h, f, and c of flowers, while *B. empetrifolia* predominates in h of spines; in all, favouring *B. Darwinii* as 19 : 13, or 59·3 per cent.

(28) *B. empetrifolia* is prepotent in h, f, and c of spines, in h, f, and

c of leaves, and in h and f of flowers, while *B. Darwinii* predominates in c of flowers; in all, favouring *B. empetrifolia* as 20 : 13, or 60·6 per cent.

(29) *B. Darwinii* is prepotent in f and c of stems, in h, f, and c of spines, and in f of leaves; in all, favouring that ancestor as 18 : 12, or 60 per cent.

(30) *B. Darwinii* is prepotent in c of stems, in f and c of spines, and in f and c of leaves, while *B. empetrifolia* predominates in h of leaves; in all, favouring *B. Darwinii* as 17 : 13, or 56·6 per cent.

In addition to the above experiments with *Berberis*, there are several cases on record which tend to show the stability of hybrids in the *Orchideæ*, *e.g.*—

Paphiopedilum × *Harrisianum*, a hybrid between *P. barbatum* (Pfitz) and *P. villosum* (Pfitz), has been raised true from seed when fertilised with its own pollen, both by Mr W. Grey, for Hon. Erastus Corning, Albany, U.S.A., and by Mr R. M. Grey, for Mr Graves, of Orange, N.Y.

M. Pauwels, of Boterlaere, France, crossed two distinct varieties of this same hybrid, which duly reproduced the specific characters of *P.* × *Harrisianum* faithfully and well.

Again, Mr W. Grey raised *P.* × *vexillarium*, a hybrid between *P. barbatum* and *P. Fairieanum* (Pfitz), from self-fertilised seed. Messrs Veitch, of Chelsea, raised *Epidendrum* × *O'Brienianum*, a hybrid between *E. radicans* (Pav.) and *E. evectum* (Hook. f.), from self-fertilised seed; but one of the seedlings, while retaining the characteristic shape of the hybrid, almost reverted *in colour* to its grandparent, *E. evectum*.

This is another illustration of Partial Prepotency, one of the grandparents being prepotent in colour only.

Dean Herbert—the great pioneer of hybridisation in this country—crossed *Petunia nictagenaeflora* with *P. phœnicea*; and the hybrid so raised reproduced itself perfectly true from seed, a large batch of seedlings being raised.

Thus the popular idea that hybrids, when self-fertilised, always revert to one or other of the ancestral species is evidently not founded on fact.

Where this is supposed to have been the case it may possibly have been due to the hybrid being accidentally fertilised with the pollen of one of the ancestral species.

THE VIGOUR OF HYBRIDS.

Most hybrids between distinct species are remarkable for their vigorous habit and large size. Many, too, are more profuse and precocious in their flowering than their parent species. But the vigour of hybrids seems to depend chiefly on their being out-crosses as opposed to being inbred. For I observe in my hybrid *Berberis* that those of the first generation, raised by crossing the two wild species, are much more vigorous than their parents; but those of the second generation, raised from the first hybrid fertilised with its own pollen, are, as a whole, less vigorous, being fairly normal in this respect. Yet my hybrid *Paphiopedilum* of the second generation, raised from a first hybrid, out-crossed again with a third species, are more vigorous even than the first hybrids, being quite abnormal in this respect. This seems to show that out-crossing continues to increase the vigour of hybrids abnormally, while inbreeding tends to reduce their vigour to a normal state.

THE LIMITS OF CROSSING.

In referring to the question of the fertility of hybrids, we saw upon what slight conditions sterility sometimes depends; and yet, if the conditions be favourable, it is remarkable what extreme forms of plants can be united by hybridisation. For instance, in the *Orchideæ*, during the past decade not only have many distinct species been successfully united, but, as we have already seen, numbers of distinct genera hybridise together with ease.

The four genera *Lælia*, *Cattleya*, *Epidendrum*, and *Sophranitis* are now all united by hybridisation, as are *Zygopetalum*, *Colax*, and *Batemannia*. These hybrids have all flowered in gardens, and show the characters of their parent genera. In addition to these are numerous records of generic crosses, yet unflowered, though plants or seeds have been produced¹ (p. 31).

The most extreme of the flowered generic hybrids in *Orchideæ* are apparently those between *Phaius* and *Calanthe*, genera belonging to distinct sub-tribes, so that the generic limit even has now been surpassed, and that of the sub-tribe reached. Is it possible to go farther than this? I think so, the relationship between many of the generic hybrids, yet unflowered, being much more remote.

I have made a number of experiments in crossing distinct genera in

¹ See *Journ. Roy. Hort. Soc.* xxi [1898], p. 468.

the Orchideæ, and, though many failures have resulted, yet some have proved rather interesting. For instance, *Sophronitis* × *Cattleya*, *Sophronitis* × *Lælia*, *Paphiopedilum* × *Phragmipedium*, *Cypripedium* × *Phragmipedium*, *Paphiopedilum* × *Cypripedium*, *Oncidium* × *Odontoglossum*, all produced healthy capsules, containing some good seeds, many of which are now germinating; while *Lycaste* × *Lælia*, *Angræcum* × *Lælia*, *Angræcum* × *Vanda*, *Paphiopedilum* × *Odontoglossum*, and *Paphiopedilum* × *Dendrobium* all produced fully developed capsules, which opened naturally in due time, but which contained no good seeds. Again, *Ada* × *Lælia*, *Cattleya* × *Angræcum*, *Dendrobium* × *Odontoglossum*, *Epidendrum* × *Dendrobium*, *Epidendrum* × *Odontoglossum*, *Cattleya* × *Dendrobium*, all produced partly formed capsules, which ultimately faded; while *Lælia* × *Lycaste*, *Dendrobium* × *Cattleya*, *Paphiopedilum* × *Cattleya*, *Epidendrum* × *Dendrobium*, and *Epidendrum* × *Paphiopedilum* all failed to set capsules.

Incompatibility of structure, apart altogether from systematic affinity, may have something to do with the limitation of crossing, for I observe in the above experiments that in all the instances where *Sophronitis* was crossed with *Cattleya*, when *Sophronitis* was the seed parent, good seeds were obtained, which duly germinated; while the reverse crosses, made at the same time and under the same conditions, in every case failed to set a capsule. Now *Sophronitis* has a very short column, while *Cattleya* has a decidedly long one, and one can quite understand that while it would be an easy matter for the pollen tubes of *Cattleya* to reach the ovules of *Sophronitis*, yet, on the other hand, it would be much more difficult for the pollen tubes of *Sophronitis* to reach the ovules of *Cattleya*, owing to the length of the column duct in the latter.

Incompatibility of colour seems to have something to do with the limitations of crossing, for Darwin gives us a large number of facts where colour varieties of the same species were more or less infertile when crossed.

The limits of crossing do not seem to be determined so much by systematic affinity or natural relationship; for, as we have seen, some very distinct genera cross with ease, while some closely allied species refuse all attempts to unite them. I have found *Oncidium flexuosum* always infertile when pollinated with its own pollen, yet quite fertile when fertilised with pollen of *O. Forbesii*, a distinct species. Nor do the limits of crossing depend upon constitutional differences, for annuals can be crossed with perennials, deciduous trees with evergreens, plants from the tropics with plants which reach to the Arctic Circle. To sum

up the whole question, we can only ascertain the true limits of crossing by actual experiments.

It is encouraging to find that the more experiments made, the more barriers there are removed, the wider become the limits of crossing. The main thing is not to be discouraged by failures, but to try again and again, and above all to keep precise records, both of the successes and the *failures*, which records may prove to be of inestimable value to science.

NOTES ON MENDEL'S METHODS OF CROSS-BREEDING¹

The first hybrid plant raised by hand appears to have been recorded by Richard Bradley in 1717 as a cross between the Carnation (*Dianthus caryophyllus* ♀) and the Sweet William (*D. barbatus* ♂), having been raised by Thomas Fairchild, of the Hoxton Nurseries near London. Since then, many hybrids and crosses in many genera have been raised by many persons in many countries. Among others, the names of Kölreuter, Knight, Herbert, Gärtner, Godron, Naudin and Darwin stand pre-eminent. The culminating point of all these being the experiments, researches and broad generalisations of Charles Darwin, which mark off a distinct epoch. The new epoch seems to have begun actually in Darwin's time, though apparently quite unknown to himself and to his contemporaries.

In 1866 (about two years before Darwin published his monumental work on the *Variation of Animals and Plants under Domestication*) Gregor Mendel published, at Brünn, the records of his remarkable experiments in cross-breeding distinct races of the Garden Pea (*Pisum sativum*)².

Curiously enough, this work remained in obscurity until 1900, when it was brought to light, almost simultaneously, by the experiments and researches of De Vries in Holland, Correns in Germany, Tschermak in Austria, and Bateson in England. So that, although 1866 marked the beginning of the new epoch, yet it was not until the last year of the

¹ Read at the Second International Conference on Hybridisation, New York City, Sept. 30th, 1902, and reprinted from *The Gardeners' Chronicle*, 1903, I. pp. 33, 34 and 76 [also published by The Horticultural Society of New York, *Memoirs Proc. Int. Conf. Plant Breeding and Hybridisation*, 1902, I. pp. 11-15 (1904)].

² "Versuche über Pflanzen-Hybriden," *Abhandl. d. Naturf. Vereins in Brünn*, 1865, IV. pp. 1-47. (See also English translation of above by the Royal Horticultural Society of London, in *Journ. Roy. Hort. Soc.* 1901, XXVI. pp. 1-32.)

nineteenth century that any marked advance was made. The psychological moment had apparently arrived, and during the past two years the progress in certain directions has been phenomenal. Experiments with various kinds of plants and animals, carried out on Mendelian lines, have yielded large numbers of facts, which, on the whole, practically confirm the results obtained by Mendel, though, at the same time, it is only fair to state that apparent exceptions are fairly numerous.

In face of these exceptions, and notwithstanding the many confirmations of Mendel's results by different observers in different kinds of plants and animals, it is quite possible that it is too early yet to regard Mendel's principles as capable of general application. At the same time, there is no doubt that Mendel's experiments and those of his disciples are a great advance on what has been done before, and will probably prove a stepping-stone towards the final solution of the problems of inheritance. For the present it may be wise to suspend our judgment and wait for further facts. But while we wait, let us also work, and help to secure those further facts, of which we are so much in need, altogether regardless of whether they happen to confirm or not the principles laid down by Mendel.

In order to accomplish this it will be necessary to work strictly on Mendelian lines, and to study Mendel's methods with great care.

Mendel, after surveying the work of his predecessors, started with a clear conception of what he wanted to investigate, and arranged his experiments accordingly.

In his own language, he wished :

- (1) To determine the number of different forms under which the offspring of hybrids appear.
- (2) To arrange these forms with certainty according to their separate generations.
- (3) To ascertain definitely their numerical or statistical relations.

The careful judgment, skill and forethought which Mendel displayed in organising and carrying out his experiments with *Pisum* were evidently the products of a master mind, and for some time to come his classical experiments will serve as a model for the hybridist who wishes to attack the perplexing problems of inheritance.

The general object of this paper is to give a brief outline of Mendel's methods, and to endeavour to show how superior they are in all respects

to the methods of his predecessors. The particular object of this paper is to express the hope that the hybridists and breeders of the New World, with their progressive ideas, their many opportunities, their vast system of experiment stations, and their practical knowledge of breeding, will take up and test the matter on a much larger scale than we can hope to do in the Old World, and thus help to bring the question to a speedy and definite issue.

So convinced is the writer of the superiority of Mendel's methods that he has already in hand a large number of experiments on Mendelian lines, in *Pisum*, *Lathyrus*, *Papaver*, *Primula*, and *Paphiopedilum* (*Cypripedium*), and also in various breeds of Fancy Poultry, the results of which he hopes to publish in due course.

MENDEL'S METHODS.

(1) *Single Characters.*

One of the most fruitful sources of confusion, in the older records of experiments in cross-breeding, has been the selection of the individual plant as the unit upon which to base the results.

The individual plant is made up of a large number of characters—organs, structures, whatever one may term them—distinctly marked off from one another, the points of difference both in form and in colour being sometimes great and at other times small. In working out the inheritance of specific characters in hybrid orchids in 1899, the writer became much impressed with the possibilities of variation in individuals, when a number of characters in each were considered together as one unit¹.

Some characters showed dominance of one parent, some of the other parent, while others were intermediate.

When these several variations occurred in twenty different characters, the possibilities of variations among the individual hybrids became very considerable, so much so that the results became quite unmanageable. Since that time the writer has been compelled to consider each *single character* on its own merits. It is true that, in some cases, the correlation of characters tends to modify this result to some extent, but in the case of the orchid hybrids in question the correlation was

¹ Report of the International Conference on Hybridisation, London, 1899, in *Journ. Roy. Hort. Soc.* 1900, xxiv. pp. 106-117. (See pp. 60-63 and 68-72.)

not very evident. From this experience it follows that in any statistics of inheritance a definite result can only be determined by taking each *single character* separately as a distinct unit, completely ignoring, for the time being, the individual plant made up of many characters.

Mendel apparently was the first to see this clearly, and acted upon it in his experiments with *Pisum*, with remarkable results.

(2) Constant Characters.

Next comes the important question of ancestry. From the earliest times it has been observed that in many instances offspring have resembled their grandparents or their more remote ancestors, rather than their actual parents. So that in experimental crossing, if two parents be chosen, each of whose ancestry is unknown or perhaps consists of complicated factors, the resulting offspring are either incomparable and incomprehensible, or they vary among themselves in bewildering confusion. The result, in any case, is chaos, and goes a long way to account for the many contradictory records which we find in the experiments carried out in the old style. Mendel, in his experiments, carefully and skilfully avoids this confusion by crossing together only *constant and fixed races*, i.e., each parent has been the product of repeated self-fertilisation, so that its ancestry has been practically the same for many generations.

This effectually eliminates all the possible complications which might be caused by the influence of the immediate ancestors at any rate, though how far it affects the possible reversion to more remote ancestors is difficult to say. The writer, in his experiments with orchids, has chosen *distinct species* only as parents, and in this way, perhaps, reduces the possibilities of reversion still more. De Vries, Correns, Tschermak and Bateson have all for the most part followed or carried out Mendel's method by crossing *constant races*, and it is quite possible that some of their apparent exceptions to Mendel's results may have been due to their crossing particular races which were not really so fixed and constant as they believed them to be.

As we have seen, Mendel carefully avoided this by selecting in the first instance fixed parents of pure descent; these he further tested for two years, and satisfied himself as to their perfect constancy and fixity,

and side by side with his crossing experiments he was careful to carry out "control" experiments with these original parents by still further testing their constancy and fixity through all the generations.

It is just possible that these precautions of Mendel may explain the general uniformity of his results as compared with those of his disciples and some of his critics¹.

(3) *Differential Characters.*

The third point worthy of note in the methods of Mendel is that the characters selected for crossing must not only be single and constant, but also *differential* in the two parents. If the single characters are nearly alike in the two parents it will be impossible to determine which parent the offspring resembles in that character, because all three would necessarily be nearly alike, *i.e.* the offspring and its two parents. On the other hand, the wider the difference between the pair of parental characters, the more clearly defined will be the single character in the resulting offspring, and consequently the easier it will be to refer the resemblance in the offspring to either parent.

Mendel, in his experiments, takes *single constant characters in the parents which are distinctly differential* and which can be clearly defined in the offspring.

(4) *Dominant Characters.*

The fourth point in Mendel's methods is distinctly new, and that is the crossing together only of *Dominant* and *Recessive* characters, *i.e.* one of the characters of the differential pairs is always distinctly dominant over the other one, which latter is known as the Recessive character.

This serves a useful purpose in giving uniformity in the first generation, and thus avoids the great difficulty of working on to the next generation with results which are not uniform.

For instance, if the pair of characters were of fairly equal potency, they would, on the whole, be intermediate—either blended or mosaic, tending to one parent and the other alternately. It is obvious, therefore, that in a case like this, if one wished to carry on the experiment to further generations, the lack of uniformity in the first generation

¹ Cf. Weldon in *Biometrika*, 1902, 1, pp. 228-254. (For complete history, exposition and Bibliography of the Mendelian question, see Bateson's admirable handbook on *Mendel's Principles of Heredity*, Cambridge University Press, 1902.)

would complicate the experiment so much as to make it almost unworkable.

Mendel avoids this by the selection of *Dominant* and *Recessive* characters only, consequently his results can easily be recorded and tabulated statistically in all the generations.

(5) *Large Numbers.*

The fifth point of note in Mendel's methods is his use of *large numbers*, and in this respect he was without doubt far in advance of his predecessors and contemporaries. In the older experiments, for the most part, only a few individuals of each cross were raised, and hence the range of variations apparent was either extreme or scarcely perceptible, according to chance and circumstances.

This no doubt accounts in some measure for the many contradictory results obtained by different experimenters at different times. Mendel avoided these difficulties by raising large numbers of individuals in each generation, and in that way practically gauged the total range of variation in each case.

(6) *Many Generations.*

Now we come to the sixth and last method of Mendel to be noted here, and that is that he was not content to stop at the first generation or even the second, as so many of his predecessors were, but he in all cases carried on the experiments to the third and fourth generations and in some cases to the fifth and sixth generations. Mendel saw clearly that this was absolutely necessary, though at the same time the work must have been very laborious, and it illustrates once more the thorough and painstaking methods by which Mendel overcame all obstacles in his pursuit of truth.

To sum up the methods of Mendel: Those hybridists who desire to follow in the footsteps of Mendel and his disciples and help to elucidate the baffling problems of inheritance will find it essential to select parents for the original cross which possess characters which are at once *Single* and *Constant* and *Differential* and *Dominant*, and they must also take care to raise *large numbers* of individuals in *many generations* for observation and comparison. By these methods alone will definite results be obtained.

In conclusion, as a practical illustration of Mendel's methods, a list is given of his own selection of characters in the *fixed races of Garden Peas* that he used for his experiments.

PISUM SATIVUM.

(Fixed Races of Garden Peas.)

<i>Mendel's Characters</i>					<i>Dominant × Recessive</i>
(1)	Form of Ripe Seeds	Round × Wrinkled
(2)	Colour of Cotyledons	Yellow × Green
(3)	Colour of Seed-Coat	} Correlated	{ Brown × White Purple × White
(3)	Colour of Flowers				
(4)	Form of Ripe Pods	Inflated × Wrinkled
(5)	Colour of Unripe Pods	Green × Yellow
(6)	Position of Flowers	Axial × Terminal
(7)	Length of Stem	6—7 ft. × $3\frac{1}{2}$ — $1\frac{1}{2}$ ft.

VI

MENDEL'S PRINCIPLES APPLIED TO ORCHID HYBRIDS¹

In previous papers I endeavoured to show the value of Orchid hybrids for observations in heredity.

As a result of these observations, the following may be laid down as a general rule:—

That in Orchid hybrids of the first generation single specific characters are inherited in all degrees of blending; forming, on the whole, a perfect series between the respective characters of the two parents.

This result in Orchid hybrids differs materially from that obtained by Mendel in his first crosses with races of Garden Peas.

In Mendel's experiments one parental character always proved dominant over the other one, giving no intermediate forms. The reason of this apparent discrepancy can, I think, be best explained on the basis of the difference between specific and racial characters. But as the question of dominance or intermediacy in the first generation is only of secondary importance, I will leave its discussion for the present, and at once proceed to that more vital question, the separation of characters in the second generation.

From both the biological and the practical points of view, the most important and far-reaching result of Mendel's experiments is the brilliant speculation by means of which he explained his practical formula for the separation of characters in the second generation.

Mendel's theory may be briefly described as follows:—

That the determinants of each single character in the germ-cells of hybrids (both pollen and egg-cells) are pure and not hybrid in their

¹ Reprinted from the *Journal of the Royal Horticultural Society*, XXVII, pp. 614-624 (1903).

nature: representing alternately the respective character either of the one parent or the other of the hybrid, but not both.

For instance, the hybrid Orchid *Paphiopedilum* \times *Leeanum* is the product of the two species *P. Spicerianum* and *P. insigne*.

According to Mendel's theory, the germ-cells of *P. \times Leeanum* will not contain hybrid determinants for any single character, but one germ-cell will contain determinants of pure *P. Spicerianum* for that character, while another germ-cell will contain determinants of pure *P. insigne* for that same character: the process being apparently according to the law of chance.

Of course, when all the single characters are taken into account together, each germ-cell would naturally contain determinants of both *P. Spicerianum* and *P. insigne*, but according to Mendel's theory there would be no determinants of the hybrid *P. \times Leeanum* itself.

This theory of Mendel is evidently quite different from anything that has been advanced before, and if proved, will undoubtedly revolutionise all previous theories of heredity.

This in its turn would materially alter the present aspect of biology toward Evolution.

It is obvious that Mendel's theory of the purity of the determinants can only be tested by experiment, and in Orchids it can be tested by breeding from the hybrid *P. \times Leeanum* or any other primary hybrid and observing the results.

Mendel tested his *Pisum* crosses in two ways only: firstly, by self-fertilisation of the first crosses, and secondly, by re-crossing the first crosses with one or other of their own parents. I have already carried out these two experiments with the hybrid *P. \times Leeanum*, but the results have not yet come to maturity: nor is there, so far as I know, sufficient material available at present to test the matter in these two ways.

But, fortunately, we are by no means confined to Mendel's two methods; there are other ways open equally reliable as a test. One of these is immediately available, and that is the crossing of the hybrid *P. \times Leeanum* with another species (distinct from its own parents), namely *P. Boxallii*.

During the past four years, forty-nine hybrids of *P. \times Leeanum* ♀ crossed with *P. Boxallii* ♂, and *vice versa*, have flowered in my collection, out of about sixty plants of that cross under raising, and these have given a fair opportunity for the study and the practical application of Mendel's





Fig. 91. \times *Paphiopedilum Hera* Kerch. vars. (*P.* \times *Leeanum* Stein (fig. 5) \times *P. Boxallii* Pfitz. (fig. 72)).
 30 F_2 Siblings, showing Mendelian segregation in three specific colour patterns of dorsal sepal.



theory. I may say in passing that there is no intrinsic difference perceptible in the reverse cross.

In accordance with the recognised rule for naming Orchid hybrids, these secondary hybrids are all to be considered forms of the original *P. × Hera*, raised by Messrs J. Veitch & Sons, of Chelsea, in 1892.

For the purpose of this paper the forty-nine individuals of *P. × Hera* will be distinguished by the numbers given them in the order in which they first flowered; though a few of them have already received varietal names on account of their horticultural merits (fig. 91).

The accompanying photographs give a good idea of the flowers of thirty of these hybrids which happened to flower together last winter. It will be noted that the variation in these hybrids is remarkable; indeed, of the forty-nine already flowered no two are exactly alike, and the extreme forms are very distinct indeed. With such a wide range of variation in all the different characters of form and colour, it is impossible to classify them with any pretence to scientific precision; but if we follow Mendel's method and select a single character, we can then group them easily.

When I first examined these hybrids in the light of Mendel, I selected, as the single character, the colour of the dorsal sepal of the flower, as this seemed to me to be the most conspicuous character, and probably the most useful one from the practical point of view of the Orchid-grower.

But after a more detailed examination of the hybrids, their parents and their grand-parents, I felt bound to come to the conclusion that the colour of the dorsal sepal could not in any sense be regarded as a single Mendelian character, but was undoubtedly a composite one, made up of three distinct characters, viz. :—

(1) The ground-colour; (2) the various markings upon the ground-colour; and (3) the median band, bar, or stripe.

These three characters seem to be inherited independently of one another, with hardly any correlation, and the different combinations of these three characters serve to make up the colour of the dorsal sepal of the flower.

Having finally selected these three single characters, each of course to be considered separately, on its own merits, the next question was to see if they fulfilled the other conditions laid down by Mendel. In Mendel's experiments he found that, to test the matter fairly and thoroughly, the characters must not only be *single*, but also *differential* and *constant*.

That each of these three characters fulfils both these conditions is evident for the following reasons:—

1. They are differential because in their nature they are specific, *i.e.* peculiar to the species, and for that reason are perhaps even more suitable for investigations in heredity than the more or less artificial races used by Mendel. At the same time it must be admitted that they have a certain disadvantage in being of the blended or intermediate type of inheritance in the first generation, rather than the dominant or exclusive type of Mendel's races.

But this disadvantage, I find, is more apparent than real, and though no doubt more complex to work out, the results are equally reliable if the investigator possesses an intimate knowledge of the material with which he is working.

2. That these specific characters are constant as well as differential and single is also obvious because they belong to natural species, whose parents and ancestors have practically been the same specifically for many generations, and thus they should be less liable to reversion or change than mere racial or varietal characters whose origin and fixation must have been comparatively recent. In other words, the question of ancestry is practically eliminated. If necessary, a further proof of this is to be found in a study and comparison of the different varieties of the three natural species with which I have been working, *viz.*:—*P. Spicerianum*, *P. insigne*, and *P. Boxallii*; all three being clear-cut and well-defined species. Of the three, *P. insigne* is certainly the most variable, covering apparently a wider area of country than the other two; but however much its varieties vary among themselves, they still all retain their specific characters intact, as do the comparatively few varieties of the other two species.

Having satisfied ourselves that the characters selected fulfil the conditions laid down by Mendel, we can at once proceed to the details of the investigation.

It will be remembered that we set out with the idea of testing Mendel's theory as to the purity of the single character determinants in the germ-cells of hybrids.

To do this, we have selected the hybrid *P. × Leeaenum* (the product of *P. Spicerianum* and *P. insigne*) and have crossed it with the species *P. Boxallii*.

For the sake of convenience and brevity we will call *P. Spicerianum*, S; *P. insigne*, I; *P. × Leeaenum*, SI; and *P. Boxallii*, B.

Our forty-nine hybrids of $P. \times$ Leeatum crossed with $P. Boxallii$ will therefore be $SI \times B$.

Now, if Mendel's theory is correct, the hybrid SI will form determinants of any single character in its germ-cells, which will be either S or I , but not SI .

Then, if SI be crossed with B , the progeny will come out for any single character, either BS or BI (on the average in equal numbers, according to the law of chance); and on the other hand they cannot come out as BSI or even SI , if Mendel's theory is correct.

In order to test the matter thoroughly it is evident therefore that, in addition to the above-mentioned species and hybrids, we must also know the characters of the collateral hybrids BS and BI , so as to be able to compare them with our hybrids of $SI \times B$. Fortunately this is comparatively easy, as large numbers of both BS and BI have been raised, figured, and described. The former, BS , the hybrid between $P. Spice-ranium$ and $P. Boxallii$, is known as $P. \times$ Calypso, and was raised by Messrs Veitch in 1891.

The latter, BI , the hybrid between $P. insigne$ and $P. Boxallii$, is known as $P. \times$ Schlesingerianum, and was first raised by Messrs Seeger & Tropp, of Dulwich, in the same year.

Specimens of these hybrids and their varieties are in my collection, so that I have been able to compare them all side by side with my $P. \times$ Hera ($SI \times B$) hybrids.

In order that readers may follow the results of my analysis of the forty-nine hybrids of $SI \times B$, and compare them for themselves by means of the photographs, I will give the details of each of the three single characters in the three original species and the three hybrids concerned, that is to say, so far as the poverty of language will permit, for it is a well-known fact that verbal descriptions, try how one may, quite fail to represent the forms and colours of Orchids as they appear to our eyes.

To those who know the species and hybrids concerned in this investigation, the accompanying photographs (fig. 91) will speak more eloquently than words.

The following are the details of the characters:—

1. *The Ground-colour of the Dorsal Sepal.*

- (a) In S this is white, with a small green area at the base.
- (b) In I it is yellow-green, with a broad white apex.
- (c) In B it is dark green up to the apex, with a narrow margin of white around the edges.

(d) In SI it is white in the upper half and yellow-green in the lower half, the size and colour of these areas varying between those of the two parents S and I.

(e) In BS it is white in the upper half and dark green in the lower half, the size and colour of these areas varying between those of the two parents B and S.

(f) In BI it is yellow-green, with white apex and margins, the size and colour of these areas varying between those of the two parents B and I.

An analysis of the 49 hybrids $SI \times B$, obtained by careful comparison with the above forms in regard to the single character of the ground-colour of the dorsal sepal, gives:—

20 BS, comparable with the various forms of $P. \times$ Calypso (BS), and 29 BI, comparable with the various forms of $P. \times$ Schlesingerianum (BI). In no case does there appear to be either a BSI or SI. In regard to this single character, therefore, the facts are apparently in accordance with Mendel's theory.

2. *The Markings upon the Ground-colour of the Dorsal Sepal.*

(a) In S these are generally absent, though there are a few claret-coloured hairs scattered over the white surface of the flower, giving it a rosy tint.

(b) In I the ground-colour, except the apex, is regularly covered with spots, which are brown on the green and purple on the white areas.

(c) In B the ground-colour, except the apex and margins, is irregularly covered with purple-black blotches, more or less confluent.

(d) In SI the ground-colour is partly covered with dots, brown on the green and purple on the white areas; these dots vary in size and number as they approach either parent, S or I.

(e) In BS the ground-colour, except the apex and margins, is covered with stripes and mottlings more or less suffused, purple-black on the green and purple on the white areas; these markings vary in size and number as they approach either parent, B or S.

(f) In BI the ground-colour, except the apex and margins, is regularly covered with large spots, black-brown on the green and dark purple on the white areas; these spots vary in size and shape as they approach either parent, B or I.

An analysis of the 49 hybrids $SI \times B$, obtained by careful comparison

with the above forms in regard to the single character of the markings on the ground-colour of the dorsal sepal, gives:—

26 BS, comparable with the various forms of *P. × Calypso* (BS), and 23 BI, comparable with the various forms of *P. × Schlesingerianum* (BI). In no case is there among the forty-nine hybrids a form approaching either SI or BSI.

As regards this single character, therefore, the facts appear to be in accordance with Mendel's theory.

3. *The Median Band, Bar, or Stripe of the Dorsal Sepal.*

(a) In S this is highly developed and clear-cut, being a solid bar of dark purple extending from base to apex.

(b) In I it is quite absent.

(c) In B it is somewhat obscure, generally irregular in outline and mostly confined to the upper middle of the dorsal sepal, and rarely extends up to the extreme apex; in colour it is purple-black, with suffused margins of purple.

(d) In SI, when present, it is usually faint, taking the form of dotted or suffused lines.

(e) In BS it is well developed from base to apex, and quite intermediate in size and colour between B and S.

(f) In BI it is either quite absent or is represented faintly by linear spots of purple-black.

An analysis of the 49 hybrids of *SI × B*, obtained by careful comparison with the above forms in regard to the character of the median band of the dorsal sepal, gives:—

30 BS, comparable with the various forms of *P. × Calypso* (BS), and 19 BI, comparable with the various forms of *P. × Schlesingerianum* (BI), there being no case of either BSI or SI.

As regards this single character, therefore, the facts are apparently in accordance with Mendel's theory.

For the sake of clearness and comparison, I have put into tabular form the details of the analyses of the three single characters, side by side, and under the respective numbers of the individual hybrids.

In this way readers may compare for themselves my analyses with the accompanying photographs, which show well the extent of the colour areas and the forms of the markings, if not the actual shades of colour, the last-named really being less differential and consequently of less importance.

ANALYSES OF FORTY-NINE HYBRIDS OF
Paphiopedilum × *Leeanum* × *P. Boxallii* = *P.* × *Hera*.

No. of Hybrid	Ground-colour	Markings on the Ground-colour	Median Band
1	BI	BS	BS
2	BI	BS	BS
3	BS	BS	BS
4	BS	BS	BS
5	BS	BS	BS
6	BI	BI	BI
7	BI	BS	BS
8	BI	BS	BS
9	BI	BS	BS
10	BI	BI	BS
11	BS	BI	BI
12	BS	BI	BS
13	BI	BI	BS
14	BI	BS	BS
15	BI	BI	BI
16	BS	BI	BI
17	BI	BS	BS
18	BI	BI	BI
19	BI	BI	BS
20	BI	BS	BS
21	BS	BI	BI
22	BI	BI	BI
23	BS	BS	BS
24	BS	BS	BS
25	BS	BI	BI
26	BS	BI	BI
27	BI	BS	BI
28	BS	BI	BI
29	BI	BS	BS
30	BS	BS	BS
31	BI	BI	BS
32	BS	BS	BS
33	BS	BS	BS
34	BI	BS	BS
35	BS	BI	BI
36	BI	BI	BI
37	BS	BS	BS
38	BS	BI	BI
39	BI	BI	BI
40	BI	BI	BI
41	BI	BI	BI
42	BS	BS	BS
43	BS	BS	BS
44	BI	BS	BS
45	BI	BS	BS
46	BI	BS	BS
47	BI	BS	BS
48	BI	BI	BI
49	BI	BI	BI
Total 49	20 BS 29 BI	26 BS 23 BI	30 BS 19 BI
Sum total 76 BS + 71 BI			

From the table it will be seen that the totals of the three single characters added together give 76 BS + 71 BI, which, considering the small numbers used, is a fair approximation to the equality which Mendel's theory presumes.

That is to say, the determinants in the germ-cells of SI are found in equal proportions of S and I, according to the law of chance. So far as these few experiments go, it may, I think, be fairly said that they confirm Mendel's theory of the purity of the determinants in the germ-cells of hybrids: that is, so far as practical results are concerned. The biologist would further require these BS and BI forms to be self-fertilised for several generations to see if they remain pure BS and BI in those characters, as they appear to be on the surface. I have arranged to carry on the experiment in this way, and have already a number of seedlings up, but I fear that some time must elapse before they arrive at the flowering stage. Those who read my previous paper on this subject (*l.c.* vol. XXVI. pp. 688—695) will be somewhat surprised at the results given above, because at that time I said that I did not see how Mendel's theory could be maintained with Orchid hybrids in face of the facts then before me.

At that time I was under the impression that the whole colour of the dorsal sepal of the flower was a single character in the Mendelian sense. A glance at the table will show that on that basis Mendel's theory could not be maintained, because, if the above three characters were taken together as a single character, the result would work out as follows: Out of the 49 hybrids there would be 11 BS + 10 BI + 28 BSI, which result would of course not be in accordance with Mendel's theory of the purity of the determinants in the germ-cells of hybrids. A short time afterwards I discovered that the apparent single character, *i.e.* the colour of the dorsal sepal of the flower, was without doubt a composite one, made up of three single characters, as detailed above. I therefore decided to postpone the publication of this paper until the hybrids flowered again, with the present result.

Just a word or two, before I conclude, on the practical aspect of Mendel's principles as applied to hybridisation in general and to Orchid hybridisation in particular. While, from the biological point of view, we cannot yet say with certainty that Mendel's principles are proved beyond doubt, yet so far as the matter has been carefully tested in many different genera, and by several independent observers in several countries, there can be no doubt that there is a substantial agreement with the principles laid down by Mendel. In these circumstances I think that the practical

hybridist would be wise to adopt Mendel's principles as a working hypothesis and base his calculations upon it. If Mendel be ultimately proved to be right, the hybridist will be justified by his results. If, on the contrary, Mendel's theory has ultimately to be modified (it cannot be altogether disproved), even then I feel sure that the hybridist will not have strayed very far from the truth, and for all *practical* purposes Mendel's principles may be safely accepted as a working formula for the hybridist in general, and the Orchid hybridist in particular.

VII

MENDEL'S PRINCIPLES APPLIED TO WHEAT HYBRIDS¹

In 1899 Prof. W. J. Spillman, of Washington, U.S.A., commenced a series of experiments in the hybridisation of two species of Wheat, *Triticum vulgare* and *T. compactum*, his primary object being to raise new varieties of good quality adapted to the climate of Eastern Washington. These experiments were continued in 1900 and 1901 and the results submitted to the Annual Convention of American Agricultural Colleges and Experiment Stations held at Washington, D.C., November 12 to 14, 1901.

The proceedings of this Convention were published in 1902, and have been kindly brought to my notice by our discerning and indefatigable Secretary, the Rev. W. Wilks, to whom I am indebted for the opportunity of making the following notes.

As will be seen hereafter, Prof. Spillman's paper is of great biological and practical importance, and as the medium through which it has been presented to the world is not very accessible to the majority of the readers of this *Journal*, I therefore venture to quote in full Prof. Spillman's tables of facts, together with his description and interpretation of them, after which I shall add a few notes of my own, showing how faithfully Prof. Spillman's facts seem to follow the Principles of Mendel. The experiments, on the whole, seem to have been admirably designed and carefully carried out, especially having regard to the large numbers used; the examination and classification of many thousands of individual characters must have entailed a vast amount of labour and care, for which we are duly grateful to Prof. Spillman and his associates. It seems fitting that this important paper should be published in the same *Journal* that first published an English translation of Mendel's original paper.

¹ Reprinted from *The Journal of the Royal Horticultural Society*, xxvii, pp. 876-893 (1903).

“QUANTITATIVE STUDIES ON THE TRANSMISSION OF PARENTAL
CHARACTERS TO HYBRID OFFSPRING.

By Prof. W. J. SPILLMAN, of Washington, U.S.A.

“Beginning in 1899, we made 14 crosses, securing, in most instances, several grains of each cross. From these grains 215 mature plants were harvested in 1900. With a few exceptions noted below, those plants of the same breeding were similar and intermediate in character between the parent forms. A head from each was preserved for future reference, the remainder of the seed being sown. The seed of each plant was kept separate, thus giving 215 plats. Of these, 149 proved to be true hybrids: the remainder were identical with the female plant, thus showing that the flowers had been self-fertilised. This is made evident by the results below.

“In each case one of the parents was of the club type (*Triticum compactum*), the other of the common type (*T. vulgare*). As above stated, no important variations occurred in the first generation except as noted below; but when the heads appeared on the second generation, a remarkable state of affairs was seen to exist. At the first glance it appeared that each of the hybrids had split up into all sorts of types. But closer inspection showed that in every case but one, which is noticed later, the forms in each plat were simply combinations of the characters of the parent forms. Further inspection revealed the fact that in plats of similar breeding exactly the same types were present. This suggested the idea that perhaps a hybrid tended to produce certain definite types, and possibly in definite proportions. Accordingly, all the hybrid plats were assorted into types, and the proportion of each type determined. When these results were classified, they confirmed the above suggestion; and if similar results are shown to follow the crossing of other groups of Wheats, it seems possible to predict, in the main, what types will result from crossing any two established varieties, and approximately the proportion of each type that will appear in the second generation. With the exceptions already referred to, the second generation consisted of the two parent types and of all the intermediate types possible between them. For instance, when one parent had long bearded heads, and the other short beardless heads, the plat could be divided into six types: two of these had long heads like one of the parents, two others short heads like the other parent, and two were intermediate; and one each of these three groups had beards, while the others had none. In some of the crosses the parent of the common form had velvet chaff,

but no beards. Here a similar set of six types appeared, the velvet replacing the beards. When one parent had velvet chaff of dark brown colour, twelve types were possible, and were actually found; six of these were similar to the six above, and the six others were like them except that they had brown chaff. As might be expected, many plants occurred more or less intermediate between these types, and it required considerable care to assort the types satisfactorily.

"Appended hereto are tables showing the percentages for all the plats that were assorted with sufficient care to be included here. To show the close agreement frequently found in the proportions in which the same types occurred in different plats, let us examine the figures for three plats of the same breeding. Type I, which was like the female parent, constituted 6 per cent. of one plat, 6·6 per cent. of another, and 6·9 per cent. of another. The percentages for the other types were as follows: II, 17·7, 17·9, and 19·1; III, 12·7, 12·4, and 13·1; IV, 40·5, 38·8, and 37·2; V, 5·7, 4·9, and 7·3; VI, which was like the other parent, 16·4, 19·5, and 19·9. The agreement is not usually so close as this, but it is fair to assume that the discrepancies are partly due to the small number of plants in each plat. They are also partly due to the fact that not a few plants were more or less intermediate between the types, and these were sometimes placed in one group and sometimes in another.

"It has been stated by nearly all investigators that there is a tendency, in the second and later generations, to revert to the parent forms. It seems possible that there is a more accurate way of stating this. The types that tend to occur in the second generation, as indicated by our results, include all possible combinations of the characters of the two parents. This, of course, includes the parent forms themselves, and we find the parent forms repeated in the second generation, constituting, apparently, certain definite portions of this generation.

"Another important fact that is clearly revealed by the tables of percentages is that the type that is most abundant in the second generation is the same as the first generation type, whether the latter is of the usual intermediate type or otherwise (see below). The exceptions to this were so rare as to render them doubtful.

"It was stated above that the first generation tends to be the same in similarly bred hybrids, and is intermediate between the parents. Let us consider the exceptions that occurred. In eleven of the fourteen crosses there were no noticeable exceptions. In one case one of four

hybrids (first generation) resembled the male parent closely, and 66 per cent. of the next generation was like it (Table III). In another case, one out of nine in the first generation differed from its fellows only in having no velvet on the chaff. In the second generation there were, in general, twelve types in these hybrids (Table XI), six with velvet and six without. The plant that was devoid of velvet in the first generation produced only the six types without velvet in the second generation. In another cross, which was the reciprocal of the last-mentioned (Table XII), nine out of the twenty-seven hybrids were more or less irregular in one or both generations. Five of the first generation were more like the female parent, and one more like the male parent than usual. In each of these cases only a few of the possible types appeared in the second generation, and the type most like the previous generation was in great excess. In two other cases the only irregularity was the unusual preponderance of the first generation type in the second generation (Plats G 19 and G 22), and the absence of several of the possible types. In five plats of this breeding bearded forms appeared, though neither parent had beards. In every case the beards appeared on heads having the form of the parent belonging to *T. vulgare*. This probably indicates the presence of bearded parents in the ancestry of the variety used [Farquahar].

“Three of the fourteen crosses were reciprocals of three of the others: *e.g.* in one case Farquahar pollen was used on Little Club (Table XI), and in another, Little Club pollen on Farquahar (Table XII). Other cases are shown in Tables I and IX, and Tables IV and XIII. The same types appeared whichever parent furnished the pollen, and in approximately the same proportions.

“While the results here reported are not sufficient to justify the positive assertion that certain quantitative laws govern the transmission of parental characters to hybrid offspring, yet they point so strongly in this direction that we may state some of these laws provisionally, looking to future investigation for their confirmation, modification, or rejection.

“That similarly bred hybrids tend to be alike in the first generation, and to be intermediate between the parent forms, and that rarely an individual resembles one parent more or less closely, has been stated by others. We may add to this, provisionally at least, the following:

“(1) In the second generation of hybrids of similar breeding (with close fertilisation) the same types tend to occur, and in definite pro-

portions; two of these types are like the parents, the others include all possible intermediate forms.

"(2) With few exceptions the most abundant type in the second generation is the same as the type found in the first generation, whether the first generation was strictly intermediate between the parents or not.

"The seed has already been sown that these studies may be continued in the third and later generations. It is hoped by continuing them to later generations to learn a good deal of a quantitative character regarding the transmission of parent characters to hybrid offspring in Wheats.

"EXPLANATION OF TABLES.

"The tables give the percentage of each type found in all plats in which this was determined. The first column gives the series and number of the plats. Type I in each case (except Table XII) is that of the parent belonging to *T. vulgare*. The last type is that of the club parent. The types are all based on certain obvious characters of the parents. In Table XII, Type IV is that of the *T. vulgare* parent, the first four types in this cross being bearded and, in this respect, unlike either parent. The figures in heavy type represent the proportion of that type most closely resembling the first generation.

"ABBREVIATIONS.

"In describing the types, the following abbreviations are used: l = heads long (*T. vulgare* type); s = heads short (*T. compactum* type); sl = semi-long = intermediate between *T. vulgare* and *T. compactum*; be = bearded; ba = bald (not bearded); br = brown chaff; li = light-coloured chaff; v = velvet chaff; g = glabrous chaff; m = male parent; f = female parent."

TABLE I.

M.—Emporium; l, br.

F.—Little Club; s, li.

Types ...	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Plat No.	l be br	l be li	l ba br	l ba li	sl be br	sl be li	sl ba br	sl ba li	s be br	s be li	s ba br	s ba li
A3	11.3	0.9	13.3	6.8	4.3	2.1	5.1	1.5	17.4	7.7	20.9	8.9
A4	4.0	1.0	16.2	5.8	3.3	4.3	15.2	3.0	9.9	3.7	32.8	8.0

TABLE II.

M.—Jones Winter Fife ; l, ba, v, li.

F.—Little Club ; s, ba, g, li.

Types	I	II	III	IV	V	VI
Plat No.	l v	l g	sl v	sl g	s v	s g
B5	20.3	6.9	39.1	12.4	15.8	5.5
B6	23.7	3.9	40.5	10.6	15.7	6.7
B7	25.6	5.2	29.2	9.3	13.9	16.7
B8	15.9	6.5	36.0	22.7	17.5	1.4
B11	24.2	8.4	37.3	6.9	16.7	6.5
B12	22.7	5.9	33.0	10.0	17.2	11.2
C1	26.4	8.8	31.2	12.0	15.0	6.6
C4	17.5	7.9	36.6	14.6	16.3	7.3
C5	11.2	4.3	42.5	15.1	21.8	6.1
C2	22.0	7.0	35.0	9.0	17.0	10.0
J16	18.7	6.2	34.0	10.3	24.6	6.8
J17	17.0	6.3	29.8	14.4	21.2	10.6
K1	19.3	8.1	36.8	11.7	17.1	6.7
K2	19.0	7.1	39.9	13.6	16.2	4.1
K3	22.9	9.1	32.0	14.3	16.7	4.7
K4	19.8	6.5	31.1	10.8	26.3	5.3
K5	21.3	6.8	29.0	15.0	21.8	6.0
K6	18.9	8.3	35.1	16.1	18.6	3.8
K8	22.4	5.7	29.2	12.5	24.5	5.7
K11	19.1	8.0	37.4	9.8	19.9	5.8
K13	18.8	7.4	39.4	13.8	14.8	5.8
L1	17.4	4.1	35.3	9.3	21.2	12.2

TABLE III.

M.—White Track ; l, ba, g, li

F.—Little Club ; s, ba, g, li.

Types	I	II	III	IV
Plat No.	l	ls-l	sl-s	s
C7	66.0	5.5	18.3	8.9
C8	30.9	7.7	45.7	16.4
C11	22.6	5.9	52.8	18.7
C12	27.1	47.5		25.4

TABLE IV.

M.—Valley ; l, be, g, li.

F.—Little Club ; s, ba, g, li.

Types	I	II	III	IV	V	VI
Plat No.	l be	l ba	sl be	sl ba	s be	s ba
C16	3.4	39.0	2.4	37.6	8.2	8.8
C18	8.5	11.9	12.7	40.6	6.0	19.5
C21	14.3	23.8	16.6	38.0	5.0	2.4

TABLE V.

M.—White Track ; l, ba, g, li.

F.—Red Chaff ; s, ba, g, br.

Types	I	II	III	IV	V	VI	VII	VIII
Plat No.	l br	l br-li	l li	sl br	sl li	s br	s br-li	s li
C10	4.4	20.6	9.5	38.4	11.1	5.0	3.2	7.0
C13	12.0	5.8	8.8	18.0	31.1	10.4	4.1	9.8

TABLE VI.

M.—McPherson ; l, ba, g, li.

F.—Red Chaff ; s, ba, g, br.

Colour of chaff disregarded in sorting.

Types	I	II	III
Plat No.	l	sl	s
E1	23.6	21.6	55.0
E9	22.8	40.0	37.3
E10	25.1	35.9	39.0
E11	33.0	29.7	37.3
E13	22.9	49.0	28.1
E14	25.0	34.0	41.0

TABLE VII.

M.—Jones Winter Fife; l, ba, v, li.

F.—Red Chaff; s, ba, g, br.

Colour disregarded in sorting.

Types	I	II	III	IV	V	VI
Plat No.	l v	l g	sl v	sl g	s v	s g
E21	15·7	10·2	50·5	11·6	11·6	0·7
E22	20·0	8·0	37·0	11·3	17·4	6·3
E24	15·6	9·9	33·1	19·2	6·3	13·5
E25	16·5	9·7	37·0	14·5	16·5	8·7
F2	25·7	6·9	41·6	13·2	8·4	4·3
F3	20·6	8·1	34·9	13·7	16·2	6·5
F11	17·3	6·8	41·4	11·7	18·4	4·5

TABLE VIII.

M.—Farquahar; l, ba, v, br.

F.—Red Chaff; s, ba, g, br.

Types	I	II	III	IV	V	VI
Plat No.	l v	l g	sl v	sl g	s v	s g
F23	23·4	8·1	41·6	12·2	11·8	5·4

TABLE IX.

M.—Little Club; s, ba, g,

F.—Emporium; l, be, g, br.

Types	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Plat No.	l be br	l be li	l ba br	l ba li	sl be br	sl be li	sl ba br	sl ba li	s be br	s be li	s ba br	s ba li
F26	1·0	3·5	8·5	5·7	3·4	0·0	34·1	7·4	11·9	3·4	11·9	9·1
F30	4·8	1·6	16·0	3·2	9·2	2·4	19·2	2·8	9·2	2·8	20·0	5·2
F31	0·7	0·0	11·6	8·1	7·0	1·0	10·5	5·8	0·0	14·0	21·1	14·0
F32	2·7	4·9	15·0	5·5	7·0	1·0	13·1	7·2	10·4	0·0	23·7	9·7
G1	10·4	0·8	10·4	6·4	8·0	0·0	6·4	5·6	0·0	0·0	20·0	20·8
G3	8·3	2·9	10·7	7·8	3·3	1·6	19·0	4·6	1·0	6·9	29·0	5·0

TABLE X.

M.—Lehigh; l, be, g, li.

F.—Red Chaff; s, ba, g, br.

Types	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Plat No.	l be br	l be li	l ba br	l ba li	sl be br	sl be li	sl ba br	sl ba li	s be br	s be li	s ba br	s ba li
F13	1·7	3·9	13·8	0·0	12·1	1·3	38·0	19·0	3·5	0·0	5·2	1·7
F15	2·0	4·5	13·5	1·5	7·7	5·0	26·3	12·7	6·4	4·7	7·0	4·7
F17	5·0	1·0	13·5	5·2	10·0	10·0	37·5	3·8	0·0	0·0	5·0	3·0

TABLE XI.

M.—Farquahar; l, ba, v, br.

F.—Little Club; s, ba, g, li.

Types	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Plat No.	l br v	l br g	l li v	l li g	sl br v	sl br g	sl li v	sl li g	s br v	s br g	s li v	s li g
I6	17·7	6·9	7·2	2·3	35·3	10·8	10·9	0·0	6·8	0·0	3·5	0·0
I7	18·2	11·3	0·0	4·5	31·3	11·3	4·5	0·0	9·1	9·1	0·0	0·0
I8	16·4	4·8	2·4	1·2	40·8	8·4	8·4	1·2	3·6	4·8	0·0	7·2
I12	13·4	2·4	0·0	3·7	35·4	6·1	9·8	0·0	11·0	6·1	7·3	4·9
I16	18·0	5·6	7·0	0·0	34·7	5·6	9·7	0·0	13·8	1·4	4·2	0·0
I17	11·7	2·6	10·4	3·9	32·5	5·2	15·6	1·3	11·7	1·3	3·9	0·0
I15	—	15·9	—	7·3	—	47·6	—	19·5	—	4·9	—	4·9

TABLE XII.

M.—Little Club; s, ba, g, li.

F.—Farquahar; l, ba, v, br.

Types	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
Plat No.	l be br v	l be br g	l be li v	l be li g	l ba br v	l ba br g	l ba li v	l ba li g	sl ba br v	sl ba br g	sl ba li v	sl ba li g	s ba br v	s ba br g	s ba li v	s ba li g
G4 ...	—	—	—	—	21.0	6.6	5.6	1.0	25.1	7.0	9.6	1.3	15.7	3.0	3.5	0.8
G5 ...	—	—	—	—	17.0	3.0	4.1	2.4	36.3	1.0	13.0	—	6.5	1.0	4.7	—
G13 ...	—	—	—	—	15.6	5.2	4.7	—	30.2	7.8	8.3	4.7	12.0	3.1	6.3	—
G14 ...	—	—	—	—	20.0	6.7	13.3	—	23.3	—	13.3	—	13.3	—	10.0	—
G16 ...	—	—	—	—	15.8	7.3	6.0	—	29.0	8.7	9.9	0.8	14.1	—	3.8	1.0
G18 ...	—	—	—	—	13.9	5.1	—	4.2	32.2	8.3	11.0	4.9	13.4	2.9	3.9	—
H2 ...	—	—	—	—	12.8	4.0	5.6	2.4	38.4	16.0	9.6	4.8	3.2	3.2	—	—
H6 ...	—	—	—	—	15.1	4.0	1.0	3.0	24.2	11.1	10.1	5.0	10.1	4.0	9.0	3.0
H7 ...	—	—	—	—	16.3	4.6	1.0	1.8	32.0	11.0	7.1	2.8	10.3	7.8	1.4	1.0
H8 ...	—	—	—	—	22.1	7.0	4.5	—	26.6	15.0	8.1	2.3	11.0	3.4	—	—
H9 ...	—	—	—	—	20.3	—	5.1	—	33.0	—	9.4	2.5	9.4	16.1	2.1	1.0
H10 ...	—	—	—	—	11.3	4.2	3.4	2.3	28.2	11.7	7.7	2.8	16.2	5.4	4.8	1.7
H11 ...	—	—	—	—	12.7	5.9	3.6	—	28.2	13.2	12.7	3.6	9.5	3.2	6.4	1.0
H12 ...	—	—	—	—	13.5	5.4	3.4	1.3	30.2	7.4	9.1	1.7	16.6	6.8	1.3	1.7
H14 ...	—	—	—	—	15.1	3.2	8.7	0.8	16.6	4.7	11.1	1.5	23.8	10.3	2.3	1.5
H15 ...	—	—	—	—	17.0	6.5	7.0	—	25.0	7.5	6.0	2.5	7.0	4.0	13.0	4.0
H16 ...	—	—	—	—	12.2	2.0	6.1	2.0	23.0	16.9	10.1	2.0	16.2	4.7	4.1	0.7
H17 ...	—	—	—	—	14.7	3.5	5.6	1.3	18.8	—	—	6.3	27.2	11.2	7.0	—
G20 ...	—	—	1.4	1.0	1.0	8.5	19.3	2.4	29.2	11.6	13.2	4.8	7.2	1.8	2.4	—
G7 ...	1.0	30.2	—	—	53.6	16.2	—	—	—	—	—	—	—	—	—	—
G9 ...	14.0	8.0	—	—	61.0	12.0	—	—	1.0	—	—	—	—	—	3.8	—
G15 ...	—	—	—	—	56.7	11.2	21.9	6.5	—	—	—	—	1.0	—	2.7	—
H1 ...	—	—	—	—	68.7	—	—	—	18.7	6.2	6.2	—	—	—	—	—
G11 ...	27.3	1.0	1.0	—	1.0	16.6	53.4	1.0	—	—	—	—	—	—	—	—
G22 ...	—	—	—	—	25.0	—	—	—	75.0	—	—	—	—	—	—	—
G19 ...	—	—	—	—	1.0	1.0	22.0	—	76.0	—	—	—	—	—	—	—
G21 ...	—	—	1.7	—	27.9	—	1.0	—	—	—	—	—	—	1.0	68.3	—

TABLE XIII.

M.—Little Club; s, ba, g, li.

F.—Valley; l, be, g, li.

Types	I	II	III	IV	V	VI
Plat No.	l be	l ba	sl be	sl ba	s be	s ba
J6	6·6	17·9	12·4	33·8	4·9	19·5
J7	7·7	22·7	13·4	37·4	3·0	15·5
I19	5·4	20·9	10·1	50·0	2·1	11·4
J3	4·7	18·1	10·0	31·8	11·5	23·6
J4	6·9	17·7	12·7	40·5	5·7	16·4
J8	6·0	19·1	13·1	37·2	7·3	19·9
J9	4·2	14·5	8·4	36·0	10·8	25·3
J10.....	3·7	13·7	17·5	36·2	3·7	25·0
J12.....	12·5	8·3	20·8	37·4	8·3	12·5
J13.....	5·4	21·9	7·1	29·6	7·1	28·5
J14.....	5·5	22·2	11·1	31·0	7·7	22·2

TABLE XIV.

M.—Turkey; l, be, g, li.

F.—Little Club; s, ba, g, li.

Types	I	II	III	IV	V	VI
Plat No.	l be	l ba	sl be	sl ba	s be	s ba
D2	8·3	19·6	26·2	20·2	6·1	19·6
D8	5·6	17·4	8·3	29·7	12·2	16·6
D9	5·2	18·4	17·5	43·3	4·4	11·4
D10	10·2	23·4	15·4	35·7	2·1	13·2
D11	3·1	21·6	21·8	39·3	3·8	10·5
D15	9·0	17·9	19·0	22·8	8·6	22·6
D16	2·6	12·2	17·7	31·0	8·8	26·7

MENDEL'S PRINCIPLES APPLIED TO PROF. SPILLMAN'S TABLES.

A glance at Prof. Spillman's tables at once suggested to me a probable confirmation of the Mendelian Principles, and a detailed analysis proved this beyond doubt.

It will be noted that in Tables III and VI Prof. Spillman takes into consideration a single character only, while in the remaining tables two or three characters are taken together. From the Mendelian point of view this is rather complicated. In order to simplify matters, I will first take each single character separately through the whole of the experiments, making a separate table for each character, and at the same time showing the percentage results as given by Prof. Spillman in his tables, with cross references thereto in the margin.

In this way complicated calculations will be avoided at the outset, and a simple result will be attained which will clearly illustrate the Mendelian Principles. The way will then be cleared for an examination of Prof. Spillman's original tables in which two or three characters are taken together.

TABLE A.

("Velvet" \times "glabrous") \times self.

Spillman's Table No.	Plat No.	"Velvet"	"Glabrous"
II	B5	75.2	24.8
	B6	79.9	21.2
	B7	68.7	31.2
	B8	69.4	30.6
	B11	78.2	21.8
	B12	72.9	27.1
	C1	72.6	27.4
	C4	70.4	29.8
	C5	75.5	25.5
	C2	74.0	26.0
	J16	77.3	23.3
	J17	68.0	31.3
	K1	73.2	26.5
	K2	75.1	24.8
	K3	71.6	28.1
	K4	77.2	22.6
	K5	72.1	27.8
	K6	72.6	28.2
	K8	76.1	23.9
	K11	76.4	23.6
	K13	73.0	27.0
	L1	73.9	25.6

TABLE A (*continued*)

Spillman's Table No.	Plat No.	"Velvet "	"Glabrous"
VII ...	E21	77.8	22.5
	E22	74.4	25.6
	E24	55.0	42.6
	E25	70.0	32.9
	F2	75.7	24.4
	F3	71.7	28.3
	F11	77.1	23.0
VIII	F23	76.8	25.7
XI	I6	81.4	20.0
	I7	63.1	36.2
	I8	71.6	27.6
	I12	77.9	23.2
	I16	87.4	12.6
	I17	85.8	14.3
XII ...	G4	80.5	19.7
	G5	81.6	7.4
	G13	77.1	20.8
	G14	93.2	6.7
	G16	78.6	17.8
	G18	74.4	25.4
	H2	69.6	30.4
	H6	69.5	30.1
	H7	68.1	29.0
	H8	72.3	27.7
	H9	79.3	19.6
	H10	71.6	28.1
	H11	73.1	26.9
	H12	74.1	24.3
	H14	77.6	22.0
	H15	75.0	24.5
	H16	71.7	28.3
	H17	73.3	22.3
	G20	73.7	30.1
	G7	54.6	46.4
	G9	76.0	23.8
	G15	82.3	17.7
	H1	93.6	6.2
	G11	82.7	18.6
Total...	60	4492.5	1490.8
Average	=	74.8	24.8
Actual ratio=3.01 : 1			
Mendelian ratio=3 : 1			

In the original cross, varieties of *T. vulgare* with "velvet chaff" were crossed with varieties of *T. compactum* with "glabrous chaff," the result being sixty-three plants with "velvet chaff" and one plant only with "glabrous chaff." In Mendelian terms the "velvet" character is Dominant, and the "glabrous" Recessive. In the next generation sixty of the "velvet" hybrids self-fertilised produced sixty plats of hybrids each containing two types, viz. Dominant and Recessive. Table A gives the approximate percentages of each type found in each plat, and it will be seen that the figures agree well with the Mendelian expectation of three Dominants to one Recessive, *i.e.* 75% "velvet" + 25% "glabrous." The average percentage of the sixty plats works out approximately 74.8 Dominants to 24.8 Recessives, *i.e.* a ratio of 3.01 : 1, being a very close approximation to the Mendelian ratio of 3 : 1. The three remaining "velvet" hybrids proved exceptional, inasmuch as, when self-fertilised, they proved practically all the same Dominant "velvet" type again (see Table XII, Plats G22, G19, G21), there being only 1% or less of the Recessive "glabrous" form. It would be interesting to know whether these forms retained their characters in future generations.

In the original cross, varieties with "brown chaff" were crossed with varieties with "light-coloured chaff," the result being forty-five hybrids with "brown chaff" and two with "light-coloured chaff." In this case the "brown" character is Dominant and the "light" Recessive. In the next generation forty-three of the "brown" hybrids self-fertilised produced forty-three plats of hybrids, each containing two types, viz. Dominant and Recessive. Table B gives the approximate percentages of each type found in each plat, and it will be seen that the figures, though not so regular as in Table A, fairly agree with the Mendelian expectation of three Dominants to one Recessive, *i.e.*

$$75\% \text{ "brown" } + 25\% \text{ "light." }$$

It seems probable that the individual plat figures are not so regular as in Table A because the character of "brown" and "light" is not so distinctly differential as "velvet" and "glabrous," and consequently more difficult to classify. However, this does not appear to have affected the average percentage of the forty-three plats, which works out approximately 73.8 Dominants to 25.4 Recessives, *i.e.* a ratio of 2.9 : 1, being a close approximation to the Mendelian ratio of 3 : 1.

The two remaining "brown" hybrids proved exceptional when self-fertilised, inasmuch as they produced the same Dominant "brown" type again, with no trace of the Recessive "light" form (see Table XII, Plats G7, G22).

TABLE B.

"Brown" x "light-coloured" x self.

Spillman's Table No.	Plat No.	"Brown"	"Light"
I	A3	72.3	27.9
	A4	81.4	25.8
V	C10	71.6	27.6
	C13	50.3	49.7
IX	F26	70.8	29.1
	F30	78.4	18.6
	F31	50.9	42.9
	F32	71.9	28.3
	G1	55.2	33.6
	G3	71.3	28.8
X	F13	74.3	25.9
	F15	62.9	33.1
	F17	71.6	28.9
XI	I6	77.5	23.9
	I7	90.3	9.7
	I8	78.8	20.4
	I12	74.4	25.7
	I16	79.1	20.9
	I17	65.0	35.1
	I15	68.4	31.7
XII	G4	78.4	21.8
	G5	64.8	24.2
	G13	74.5	24.9
	G14	63.3	36.6
	G16	74.9	21.5
	G18	75.8	24.0
	H2	77.6	22.4
	H6	68.5	31.4
	H7	82.0	15.1
	H8	85.1	14.9
	H9	78.8	20.1
	H10	77.0	22.7
	H11	72.7	27.3
	H12	79.9	18.5
	H14	73.7	25.9
	H15	67.0	32.5
	H16	75.0	25.2
	H17	75.4	20.2
	G20	59.3	44.5
	G9	96.0	3.8
	G15	68.9	31.1
	H1	93.6	6.2
	G19	78.0	22.0
Total	43	3176.0	1096.0
Average	=	73.8	25.4
Actual ratio=2.9 : 1		Mendelian ratio=3 : 1	

It will be noted that Plat G 22 was also one of the exceptions under Table A.

In the original cross, varieties with "bald heads" were crossed with varieties with "bearded heads," the result being thirty hybrids with "bald heads" and none with "bearded heads." In this case the "bald" character is Dominant and the "bearded" Recessive. In the next generation the thirty "bald" hybrids self-fertilised produced thirty plats of hybrids, each containing two types, viz. Dominant and Recessive. Table C gives the approximate percentages of each type found in each plat, and it will be seen that, with a few exceptions, the figures fairly agree with the Mendelian expectation of three Dominants to one Recessive, *i.e.*

$$75\% \text{ "bald" } + 25\% \text{ "bearded."}$$

The average percentage of the thirty plats works out approximately 72.1 Dominants to 26.5 Recessives, *i.e.* a ratio of 2.7 : 1, which is approximate to the Mendelian ratio of 3 : 1.

That the average result in this case is not so close to Mendel as in the two former tables is probably due to the smaller number of plats involved.

There are apparently no exceptions in regard to the Dominance of "bald" in the original cross, though it is interesting to note that in Table XII, where two "bald" varieties are crossed together, giving twenty-seven "bald" hybrids, these hybrids self-fertilised produced a small percentage of "bearded" hybrids in five plats out of the twenty-seven, thus suggesting that one of the varieties used in this cross was not pure and constant. If this be so, it may possibly explain the few exceptions noted under Tables A, B, and D, as these all apparently occur in that particular cross (Table XII).

In the original cross, varieties of *T. vulgare* with "long heads" were crossed with varieties of *T. compactum* with "short heads," the result being ninety-seven "intermediate" or "semi-long," six "long," and five "short." This result, it is important to notice, differs from Mendel's experiment with Peas, inasmuch as the first generation is "intermediate" between the parents, with no Dominance of either parent. But, as will be seen in Table D, in the second generation the Mendelian Principles work out admirably.

In the second generation, ninety-five of the intermediate hybrids self-fertilised produced ninety-five plats of hybrids, each containing three types, viz. "long," "intermediate," and "short," *i.e.* the two original forms and intermediate forms, the last being twice as numerous as

TABLE C.

("Bald" \times "bearded" heads) \times self.

Spillman's Table No.	Plat No.	"Bald"	"Bearded"
IV	C16	85.4	14.0
	C18	72.0	27.2
	C21	64.2	35.9
IX	F26	76.7	24.2
	F30	66.4	30.0
	F31	71.1	22.7
	F32	74.2	26.0
	G1	69.6	19.2
	G3	76.1	24.0
X.....	F13	77.7	22.5
	F15	65.7	30.3
	F17	68.0	26.0
XIII ...	J6	76.2	23.9
	J7	75.6	24.1
	I19	82.3	17.6
	J3	73.5	26.2
	J4	74.6	25.3
	J8	76.2	26.4
	J9	75.8	23.4
	J10	74.9	24.9
	J12	58.2	41.6
	J13	80.0	19.6
XIV ...	D2	59.4	40.6
	D8	63.7	26.1
	D9	73.1	27.1
	D10	72.3	27.7
	D11	71.4	28.7
	D15	63.3	36.6
	D16	69.9	29.1
Total	30	2162.9	795.2
Average	=	72.1	26.5

Actual ratio = 2.7 : 1

Mendelian ratio = 3 : 1

either of the others. Table D gives the approximate percentages of each type found in each plat, and it will be seen that with a few exceptions the figures fairly agree with the Mendelian expectation of $A + 2Aa + a$, *i.e.* 25 % "long" + 50 % "intermediate" + 25 % "short." The average percentage of the ninety-five plats works out approximately 26.5 "long" + 48.2 "intermediate" + 24.5 "short," being a close approximation to the Mendelian ratio of 25 : 50 : 25.

This case is peculiarly interesting from the practical point of view, as it shows that normal intermediate hybrids of the blended type of inheritance also separate their characters in accordance with the Mendelian Principles, thus confirming what the writer has already shown in orchid hybrids (pp. 99—108), *viz.* that Mendel's Principles do not depend at all upon the question of Dominance in the first generation, which latter is merely a phase of inheritance, the actual causes of which are at present not quite clear, though it seems probable that there is some connection between inbred races and Dominance.

TABLE D.

("Long" × "short" heads) × self.

Spillman's Table No.	Plat No.	"Long"	"Inter- mediate"	"Short"
II	B5	27.2	51.5	21.3
	B6	27.6	51.1	22.4
	B7	30.8	38.5	30.6
	B8	22.4	58.7	18.9
	B11	32.6	44.2	23.2
	B12	28.6	43.0	28.4
	C1	35.2	43.2	21.6
	C4	25.4	51.2	23.6
	C5	15.5	57.6	27.9
	C2	29.0	44.0	27.0
	J16	24.9	44.3	31.4
	J17	23.3	44.2	31.8
	K1	27.4	48.5	23.8
	K2	26.1	53.5	20.3
	K3	32.0	46.3	21.4
	K4	26.3	41.9	31.6
	K5	28.1	44.0	27.8
	K6	27.2	51.2	22.4
	K8	28.1	41.7	30.2
	K11	27.1	47.2	25.7
	K13	26.2	53.2	20.6
	L1	21.5	44.6	33.4

TABLE D (continued)

Spillman's Table No.	Plat No.	" Long "	" Inter- mediate "	" Short "
III	C8	30.9	53.4	16.4
	C11	22.6	58.7	18.7
	C12	27.1	47.5	25.4
IV	C16	42.4	40.0	17.0
	C18	20.4	53.3	25.5
	C21	38.1	54.6	7.4
V.....	C10	34.5	49.5	15.2
	C13	26.6	49.1	24.3
VI	E9	22.8	40.0	37.3
	E10	25.1	35.9	39.0
	E13	22.9	49.0	28.1
	E14	25.0	34.0	41.0
VII.....	E21	25.9	62.1	12.3
	E22	28.0	48.3	23.7
	E24	25.5	52.3	19.8
	E25	26.2	51.5	25.2
	F2	32.6	54.8	12.7
	F3	28.7	48.6	22.7
	F11	24.1	53.1	22.9
VIII	F23	31.5	53.8	17.2
IX	F26	18.7	44.9	36.3
	F30	25.6	33.6	37.2
	F31	20.4	24.3	49.1
	F32	28.1	28.3	43.8
	G1	28.0	20.0	40.8
	G3	29.7	28.5	41.9
X.....	F13	19.4	70.4	10.4
	F15	21.5	51.7	22.8
	F17	24.7	61.3	8.0
XI	I6	34.1	57.0	10.3
	I7	34.0	47.1	18.2
	I8	24.8	58.8	15.6
	I12	19.5	51.3	29.3
	I16	30.6	50.0	19.4
	I17	28.6	54.4	16.9
	I15	23.2	67.1	9.8

TABLE D (continued).

Spillman's Table No.	Plat No.	" Long "	" Inter- mediate "	" Short "
XII.....	G4	34.2	43.0	23.0
	G5	26.4	42.3	12.2
	G13	25.5	51.0	21.4
	G14	40.0	36.6	23.3
	G16	29.1	48.4	18.9
	G18	23.2	56.4	20.2
	H2	24.8	68.8	6.4
	H6	23.1	50.4	24.1
	H7	23.7	52.9	20.5
	H8	33.6	52.0	14.4
	H9	25.4	44.9	28.6
	H10	21.4	50.4	28.1
	H11	22.2	57.7	20.1
	H12	23.6	48.4	26.4
	H14	27.8	33.9	37.9
	H15	30.5	41.0	28.0
	H16	22.3	52.0	34.7
	H17	25.1	25.1	45.4
	G20	33.6	58.8	11.4
XIII ...	J6	24.5	51.2	24.4
	J7	30.4	50.8	18.5
	I19	26.3	60.1	13.5
	J3	22.8	41.8	35.1
	J4	24.6	53.2	22.1
	J8	25.1	50.3	27.2
	J9	18.7	44.4	36.1
	J10	17.4	53.7	28.7
	J12	20.8	57.4	20.8
	J13	27.3	36.7	35.6
	J14	27.7	42.1	29.9
XIV ...	D2	27.9	46.4	25.7
	D8	23.0	38.0	28.8
	D9	23.6	60.8	15.8
	D10	33.6	51.1	15.3
	D11	24.7	61.1	14.3
	D15	26.9	41.8	31.2
	D16	14.8	48.7	35.5
Total...	95	2519.9	4585.4	2330.4
Average	26.5	48.2	24.5
Mendelian ratio ... 25 : 50 : 25				

Formerly it was thought that the Mendelian Principles were only applicable to Dominant hybrids and crosses, but now that intermediate hybrids are being brought into line, and as they appear to be generally more numerous than Dominant hybrids, it seems likely that the Mendelian Principles will ultimately be extended to cover all the phenomena of hybridisation and cross-breeding. At the same time it should be clearly recognised that there are undoubtedly many complications existing which were not fully known to Mendel, and which future experiments alone can unravel.

The remaining two intermediate hybrids, when self-fertilised, proved slightly exceptional, inasmuch as they produced no "short" forms at all, but simply 75 % "intermediate" and 25 % "long" (see Table XII, Plats G22 and G19). It will be noted, again, that the exceptions only occur in one cross, Table XII, and that Plat G22 is exceptional in all three characters, while Plat G19 is exceptional in two characters out of three, all of which lends colour to the suggestion made under Table C, that one of the varieties of this cross is not truly pure and constant in its characters.

Having dealt with the behaviour of all the "Dominant" hybrids, we now come to the consideration of those few forms which in the original cross showed the "Recessive" form rather than the usual "Dominant." In other words, the "Recessive" becomes Dominant, and the "Dominant" Recessive. This may at first sight appear to be a small matter, and one which Mendel does not seem to have experienced, but it appears to me to be of great importance, as it touches the vital question of *individual* versus *ancestral* inheritance.

In Prof. Spillman's experiments, there appear to have been fourteen cases in the four characters, out of a total of 249, and these when self-fertilised seem to have given two different results: viz. in six cases the "Recessive" character was again reproduced almost pure, and in the remaining eight cases in the approximate proportion of 75 % "Recessive" to 25 % "Dominant." (For details see Table I, Plats A3, A4; III, C7; VI, E1, E11; XI, I15; XII, G7, G9, G15, H1, G11, G21.)

It will again be noted that all the six cases in which the Recessive remained almost pure occurred in the same cross (Tables XI and XII) which gave the exceptions to the Mendelian cases. Disregarding these, therefore, and looking at the remainder of Prof. Spillman's facts, it would appear that *the Mendelian Principles are followed in every case, but that the second generation tends to repeat in Mendelian proportions*

whatever is shown by the first generation, whether "Dominant," Intermediate, or "Recessive."

That is to say, if the individuals of the first generation are of the "Dominant" type, they will reproduce that type in the second generation in the ratio of 3D : 1R; but if they happen to be of the "Recessive" type they will reproduce that same type in the second generation in the ratio of 3R : 1D; while if the individuals of the first generation are of the Intermediate type, they will reproduce that type in the second generation in the ratio of 1D : 2DR : 1R.

If future experiments confirm this, it will be an important advance in our knowledge of heredity, and to the practical hybridist the information will be invaluable, as he will be able to select whatever he wants in the first generation, whether it happens to be "Dominant," Intermediate, or "Recessive," and by the aid of the Mendelian Principles he will be able to calculate the result beforehand.

Having dealt hitherto simply with single characters, and found them to be strictly Mendelian, we now proceed to the much more complicated question of two and three characters taken together. For this purpose Prof. Spillman's tables are admirable and require no analysis: we can take them as they stand in his original paper.

First we will take those tables in which two characters are considered together.

In Tables II, VII, and VIII, varieties with "long heads" and "velvet chaff" were originally crossed with varieties with "short heads" and "glabrous chaff," the result being thirty hybrids with "intermediate heads" and "velvet chaff." These thirty hybrids, self-fertilised, produced thirty plats, each containing six types, on the average in the following proportions, viz.

$$10.9(1 + v) + 7.2(1 + g) + 36.2(sl + v) + 12.7(sl + g) \\ + 17.2(s + v) + 6.8(s + g).$$

Now, if we take the Mendelian formulæ for the two single characters, we get for the one $11 + 2sl + 1s$, and for the other $3v + 1g$.

Now the possible combinations between them would be six, in the following proportions, viz.

$$3(1 + v) + 1(1 + g) + 6(sl + v) + 2(sl + g) + 3(s + v) + 1(s + g),$$

the approximate percentage of which would be respectively

$$18 + 6 + 36 + 12 + 18 + 6.$$

This Mendelian expectation agrees well with the actual percentages respectively of Prof. Spillman's experiments given above, viz.

$$19.9 + 7.2 + 36.2 + 12.7 + 17.2 + 6.8.$$

In Tables IV, XIII, and XIV, varieties with "long" and "bearded heads" are crossed with varieties of "short" and "bald heads," the result being twenty-one hybrids with "intermediate bald heads." These twenty-one hybrids, self-fertilised, produced 21 plats, each containing six types, on the average in the following proportions, viz.

$$6.6 (l + be) + 19.1 (l + ba) + 14.0 (sl + be) + 35.4 (sl + ba) \\ + 6.5 (s + be) + 17.7 (s + ba).$$

The Mendelian formulæ for the two single characters are respectively $1l + 2sl + 1s$ and $3ba + 1be$, and the possible combinations between them would be six, in the following proportions, viz.

$$1 (l + be) + 3 (l + ba) + 2 (sl + be) + 6 (sl + ba) + 1 (s + be) + 3 (s + ba),$$

the approximate percentages of which would be respectively

$$6 + 18 + 12 + 36 + 6 + 18.$$

This Mendelian expectation agrees well with actual percentages respectively of Prof. Spillman's given above, viz.

$$6.6 + 19.1 + 14.0 + 35.4 + 6.5 + 17.7.$$

It is quite evident, therefore, that the Mendelian Principles apply to two characters taken together as well as to single characters taken separately, though the expression of them is naturally more complicated.

Secondly, we will consider the still more complicated case of three characters taken together. In Tables XI and XII a variety with "long heads" and "brown velvet chaff" is crossed with a variety with "short heads" and "light-coloured glabrous chaff." The result is twenty hybrids with "intermediate heads" and "brown velvet chaff." These twenty hybrids self-fertilised produced twenty plats containing twelve types, on the average in the following proportions, viz.

$$16.1 (l + br + v) + 5.1 (l + br + g) + 4.4 (l + li + v) + 1.6 (l + li + g) \\ + 31.3 (sl + br + v) + 8.3 (sl + br + g) + 9.8 (sl + li + v) \\ + 1.9 (sl + li + g) + 10.8 (s + br + v) + 4.1 (s + br + g) \\ + 3.8 (s + li + v) + 1.6 (s + li + g).$$

The Mendelian formulæ for the three single characters are respectively

$$1l + 2sl + 1s, \quad 3br + li, \quad \text{and} \quad 3v + 1g,$$

and the possible combinations between these would be

$$\begin{aligned} &9(l + br + v) + 3(l + br + g) + 3(l + li + v) + 1(l + li + g) \\ &\quad + 18(sl + br + v) + 6(sl + br + g) + 6(sl + li + v) \\ &\quad + 2(sl + li + g) + 9(s + br + v) + 3(s + br + g) \\ &\quad + 3(s + li + v) + 1(s + li + g), \end{aligned}$$

the approximate percentages of which would be respectively

$$13.5 + 4.5 + 4.5 + 1.5 + 27.0 + 9.0 + 9.0 + 3.0 + 13.5 + 4.5 + 4.5 + 1.5.$$

This Mendelian expectation agrees fairly with the actual percentages respectively of Prof. Spillman's given above, viz.

$$16.1 + 5.1 + 4.4 + 1.6 + 31.3 + 8.3 + 9.8 + 1.9 + 10.8 + 4.1 + 3.8 + 1.6.$$

It is quite evident, therefore, that the Mendelian Principles apply equally to three characters taken together as well as to two characters and to single characters, though the expression is necessarily much more complicated.

Prof. Spillman's facts, on the whole, as he himself says, prove to the practical hybridist that in the self-fertilisation of first-crosses between constant varieties it is possible to know beforehand exactly what types will be obtained, and further to calculate the average percentage of each. It reflects the greatest possible credit on Prof. Spillman that he should have arrived at this result independently, not having apparently heard of Mendel's work on similar lines, and the thanks of all hybridists are due to him for his independent confirmation of Mendel's Principles¹.

(Since the above paper was sent to the press Mr Bateson has kindly drawn my attention to a further paper by Prof. Spillman in *Science*, 1902, xvi. p. 794, in which he himself clearly notes the Mendelian significance of his experiments.—C. C. H.)

¹ The late Sir Francis Galton, F.R.S., in a letter dated June 18th, 1903, writes:—"Thank you much for your important memoir on Wheat Hybrids. I have studied and shall re-study it carefully. As a small criticism of I believe *no practical* importance here, the 'Mean of Means' is a questionable statistical process and though the only method practicable here, its imperfection might with advantage have been hinted. If the means had severally been those of the same number of individuals the result would of course be strictly correct, otherwise the several means are not of equal weight, and the mean (for example) of two cases exercises as much influence on the Result as the mean of two hundred or more cases. I merely point this out to suggest the insertion of a deprecatory paragraph, if you reprint this memoir, *not* because I think it can influence your conclusions in a sensible degree."



Fig. 92. × Calanthe Dominii Lindl.
The first hybrid orchid raised by hand (1856).
(*Orchid Review*.)

VIII

EXPERIMENTS IN THE HYBRIDISATION OF ORCHIDS¹

The first hybrid Orchid raised by hand was *Calanthe* × *Dominii* (fig. 92), which flowered with Messrs Veitch at Exeter, in 1856, out of *C. Masuca* by pollen of *C. furcata*. Since then, and especially during the last decade, the number of hybrid Orchids has increased remarkably, until at the present time there are on record more than 1300, each representing a distinct cross. Of these at least 230 are generic hybrids, while the individuals of each cross are innumerable. The great majority, too, are fertile and comprise hybrids of the second, third, and fourth generations. One of the more advanced of these is *Paphiopedilum* × *Kubele*, which contains five distinct species in its pedigree. It is evident therefore that in many respects Orchids offer a wide field to the student of inheritance.

INTERMEDIATE HYBRIDS.

My own experiments in Orchids have been mainly confined to the hybrids between three Indian species of *Paphiopedilum* (formerly known as *Cypripedium*)—viz. *P. Spicerianum*, from Assam; *P. insigne*, from Nepal; and *P. Boxallii*, from Burma. For brevity I will term these S, I, and B respectively, and for simplicity I will deal with a single conspicuous character in each—viz. the colour-markings on the dorsal sepal of the flower. In B these take the form of purple-black blotches more or less confluent. In I they are round regular spots, brown on the green and purple on the white ground. In S these colour-markings are absent. In the first generation (F_1 of Bateson) S was crossed with I, and *vice versa*, giving about fifty hybrids, known as *P. × Leeaeum*, which I will term SI. The result was practically the same in both crosses, the colour-markings taking the form of a few small regular dots, brown on

¹ Paper read before Section K at the Southport Meeting of the British Association for the Advancement of Science, Sept. 12th, 1903. Reprinted from *Gardeners' Chronicle*, 1903, II. pp. 226–227.

the green, and purple on the white ground, thus being fairly intermediate between the spotted I and the unspotted S. Individuals from the same capsule varied slightly in the size and number of the dots, as they tended towards the I or S parent. This result is a good illustration of the intermediate or blended type of inheritance which prevails in the great majority of Orchid hybrids. In the second generation (F_2), one of the SI hybrids was crossed with the third species B, and *vice versa*, giving about sixty hybrids known as $P. \times$ Hera, of which forty-nine have flowered, and thirty have been figured (Hurst, 1903) (fig. 91).

So far as the colour-markings are concerned, these forty-nine hybrids fall naturally into two distinct groups. The first group, twenty-three in number, consists wholly of spotted forms, the colour-markings taking the form of numerous irregular but distinct spots, black on the green, and dark purple on the white ground.

The second group, twenty-six in number, consists wholly of lined forms, the colour-markings taking the form of suffused lines and stripes, black on the green and dark purple on the white ground. These two groups are apparently discontinuous, so that each hybrid falls naturally into one group or the other, each group having its own set of individual variations. Careful comparison shows that the first or "spotted" group resembles the collateral F_1 hybrid BI, known as $P. \times$ Schlesingerianum (Boxallii \times insigne); while the second or "lined" group resembles the collateral F_1 hybrid BS, known as $P. \times$ Calypso (Boxallii \times Spicerianum). These F_1 hybrids, BI and BS, are unmistakably distinct from one another, though individually variable in this particular character; and these same variations are practically repeated in the F_2 hybrids $SI \times B$.

Hence we see that for a single character $SI \times B = BI + BS$. As it is with this character so it is with the other characters so far as they have been observed. These results are a further confirmation of the Mendelian idea of the separation of hybrid characters. According to Mendel the F_1 hybrid SI should for any single character produce pure S and pure I gametes in equal numbers, and not any hybrid SI gametes at all, so that in F_2 , when SI is crossed with B, the pure B gametes will unite alternately with the pure S and the pure I gametes, and the resulting zygotes will be BS and BI in equal numbers. As we have seen, the actual result is 23 BI + 26 BS, which is near to equality considering the small numbers involved. It is evident, therefore, that the phenomena of the separation of hybrid characters, so brilliantly demonstrated by Mendel in *Pisum*, may also be observed in intermediate Orchid hybrids.

DOMINANT HYBRIDS.

So far the hybrids dealt with belong to the intermediate or blended type of inheritance, as do the great majority of Orchid hybrids. In certain distinct crosses, however, we find that one parent is always dominant in all characters, almost to the exclusion of the other. For example, *Epiphrontis* × *Veitchii*, raised by Messrs Veitch in 1890 out of *Sophrontis grandiflora* by pollen of *Epidendrum radicans*, is in all its structural characters a pure *Epidendrum*; the only traces of the *Sophrontis* parent being the dwarfer habit, fewer larger and darker flowers, with a few slight modifications of the lip and crest. Indeed, did we not know that *Sophrontis* was the other parent, it would have been impossible to have suggested it. In addition to the above, more than twenty distinct hybrids have been raised between various species of *Epidendrum* with reed-like stems, and various species of *Epidendrum*, *Lælia*, *Cattleya*, and *Sophrontis* with pseudo-bulbs, comprising thousands of individuals, and all without exception have the reed-like stems and general characters of *Epidendrum* (cf. Hurst, 1898 and 1900, and pp. 32 and 65). Unfortunately these hybrids have so far proved infertile, their pollen being apparently defective and actually impotent. We cannot therefore test their nature by further breeding, and it is impossible to say whether they are comparable to Mendel's cases of dominance in *Pisum*.

FALSE HYBRIDS.

We now come to those curious cases of one-sided inheritance in Orchids to which I have applied Millardet's term of "false hybrids" (1900, p. 105). The most numerous of these are the various crosses that have been attempted by expert hybridists at different times and in different countries, between *Zygopetalum* and several more or less remote genera, with the result that all the offspring have proved to be *Zygopetalum* pure and simple. Altogether more than 400 seedlings have been raised by Messrs Veitch of Chelsea, Heath of Cheltenham, Bleu of Paris, Ross of Florence, Leon of Bletchley, Orpet of S. Lancaster, U.S.A., McWilliam of Whitinsville, U.S.A., and the Rev. Horner of Kirkby Lonsdale. The seed-parent in each case was *Zygopetalum Mackayi* (the reverse crosses being unsuccessful). The pollen used was from *Odontoglossum Pescatorei*, *O. crispum*, *O. grande*, *O. bicktonense*, *Oncidium tigrinum*, *Lycaste Skinneri*, *Lælia anceps*, *Calanthe vestita*, and *Vanda cœrulea*. All the 400 seedlings raised from these matings proved to be exactly like the seed-parent, *Z. Mackayi*. It is

interesting to note, however, that the individuals raised from the same capsule varied in size and colour of the flowers in the same way that the seed-parent species does in its native habitat.

In other words, the "false hybrids" behaved just as if they had been raised from self-fertilised seeds, but, as I showed in 1898, self-fertilisation, direct or indirect, was impossible in these cases, as the pollinia of the seed-parents were all carefully removed before the crosses were made (1898, p. 477). Apart from this, too, the peculiar structure of these Orchids makes self-fertilisation impracticable, as Darwin has well shown (1862, p. 150, f. 23). Nor is it apparently a case of Mendelian dominance, for in the second generation (F_2) the characters of the seed-parent are again repeated pure and simple, even when the "false hybrid" is re-mated with the supposed recessive. This experiment was carried out by Mr McWilliam, by re-mating one of the F_1 "false hybrids" (*Z. Mackayi* ♀ × *L. anceps*) with pollen of *L. anceps alba*, and the result was still *Z. Mackayi* pure and simple.

It seems clear, therefore, that we have in these *Zygopetalum* seedlings, "false hybrids," comparable to the original ones of Millardet in *Fragaria* (1894). It may be noted that all the "false hybrids" in Orchids so far are maternal in all characters, as were the majority of Millardet's (1894), and also Bateson and Saunders' *Matthiola* (1902, p. 79).

Other experiments, however, show that "false hybrids" may occur that are paternal in all characters, as in a few of Millardet's *Fragaria* (1894), and De Vries *Oenothera* (1903, p. 31). The most interesting cases of "false hybridism" are, however, only just coming to light both in plants and animals, in which a single character only behaves as a "false hybrid," the remaining characters being true hybrids.

These may be purely maternal in one character, as in Bateson's *Single comb Poultry* (1902, p. 115), and apparently in Spillman's *glabrous and long-headed Wheats* (1902, p. 97); or they may be purely paternal in one character, as in Bateson's *Single-comb Poultry* (1902, p. 115), and my own unpublished experiments with plumage colour in poultry.

Whether all these types of "false hybrids" have a common explanation is difficult to say, but so far as the *Zygopetalum* series is concerned, in 1900 I suggested that the stimulus of fertilisation might induce a kind of parthenogenesis, without actual union of the sexual elements (1900, p. 106), causing the "false hybrids" to resemble the seed-parent in all characters. This idea has been favourably received by Bateson

(1902, p. 157) and De Vries (1903, p. 31), and it seems quite feasible that an extension of it may ultimately explain all the phenomena of "False Hybridism," or Monolepsis, as Bateson more precisely terms it (1902, p. 155).

In conclusion, there is no doubt that the question of "False Hybridism," or Monolepsis, opens out a wide field for original research in many genera of plants and animals; and as our knowledge of normal inheritance increases, the need for experiments into the nature of one-sided inheritance becomes more urgent and pressing.

REFERENCES.

- BATESON AND SAUNDERS (1902). *Rep. Evol. Com. Roy. Soc.* I.
 DARWIN (1862). *Fertilisation of Orchids* (2nd edit.).
 DE VRIES (1903). *Die Mutations Theorie*, II.
 HURST (1898). *Journ. Roy. Hort. Soc.* XXI. pp. 442-486.
 — (1900). *Journ. Roy. Hort. Soc.* XXIV. pp. 90-126.
 — (1903). *Journ. Roy. Hort. Soc.* XXVI. pp. 614-624.
 MILLARDET (1894). *Mém. Soc. Sci. Bordeaux*, IV. p. 347.
 SPILLMAN (1902). *Bull.* 115, *Ex. Sta. U.S. Dept. Agr.* pp. 88-98.

IX

MENDEL'S DISCOVERIES IN HEREDITY¹

Gregor Johann Mendel was born in Austrian Silesia in 1822. In 1843 he entered the cloister of an Augustinian foundation in Altbrünn, and was ordained priest in 1847. From 1851 to 1853 he studied the natural sciences at Vienna, and on his return to the cloister became a teacher in the Realschule at Brünn.

In 1854, Mendel commenced his remarkable series of experiments with Peas in the gardens of his cloister, and continued them for about ten years. In 1865 he communicated his facts and discoveries to the Brünn Society of Naturalists, and his paper was published in the journal of that Society in 1866. Mendel appears to have continued his experiments, for in 1869 he communicated a preliminary account of some *Hieracium* hybrids to the same Society, but about this time he was made Abbot of Brünn, and apparently could not find time to complete his experiments and elaborate his discoveries. In his later years he took a leading part in local racial controversies, and at last died at Brünn, in 1884, practically unknown to science. Such is the plain outline of Mendel's life, which, with our present knowledge of his brilliant discoveries, seems almost pathetic. Mendel's work remained practically unknown to science not only during his life-time, but for 16 years after his death. It is true that there is a single brief reference to his paper in Focke (1881, p. 109), but with no recognition of its value. ¶ It was not until 1900 that Mendel's paper was re-discovered, experimentally confirmed, and made known to science by Professor Hugo de Vries some 35 years after it was communicated to the Brünn Society. ¶ The story of the almost simultaneous discovery and experimental confirmation of Mendel's work by De Vries in Holland (1900 *b* and *d*); Correns, in Germany (1900 *a* and *b*), and Tschermak in Austria (1900) reads like a romance. What would have happened had Mendel's work come into the hands of Darwin, no one can say, but there is little doubt that had it been so, the popular ideas of heredity, variation, and evolution would have been widely different from what they are to-day. Apart from Mendel, the history of heredity in the nineteenth century is

¹ Read before Section "E" of the Leicester Literary and Philosophical Society, and reprinted from the *Transactions of the Leicester Literary and Philosophical Society*, VIII. Part II. June, 1904, pp. 121-134.

little more than a mass of confused and apparently contradictory results, which Darwin (1868) in his monumental work, *Animals and Plants*, courageously and patiently attempted to reduce to order.

It is easy to be wise after the event, but as we look now, in the light of Mendel, we can see at once why Darwin and his predecessors failed to discover a law of heredity. Theories there were in plenty, but not one law. It was mainly by the simplicity of his methods that Mendel succeeded in discovering a law of heredity. With keen insight he concentrated his experiments on one kind of plant, dealt with simple characters *singly*, worked with large numbers *individually*, and continued his experiments through several generations.

In this way he was able to discover the law of heredity which will always be associated with his name, and which bids fair to revolutionise the modern conceptions of biology.

After several experiments with different kinds of plants, Mendel finally selected the garden Pea (*Pisum sativum*) as a suitable subject, and in this selection he was amply justified by his results.

The garden Pea offers many advantages to the experimenter. Most of the races are constant, breeding true to type, and many of the characters are distinct and discontinuous; owing to dominance the hybrids of the first generation are, as a rule, uniform, and the hybrids are fully fertile in all the generations. The flowers of the Pea are naturally self-fertilised before the bud opens, so that insects do not disturb the results when the flowers are left uncovered. The emasculation of the flower bud is easy and the pistil being ripe before the stamens, the foreign pollen can be applied at once, and in sufficient quantity to prevent other pollen affecting the result.

The Pea being an annual, a generation can be raised in a year, large numbers can be grown in a small garden, and last but not least, two characters, *seed-shape* and *seed-colour*, can be determined a few weeks after the cross is made, so that two generations of these can be observed in a little more than a year after the first crossing, and so on, through all the generations.

Mendel dealt with seven pairs of differential characters in Peas, viz. Round and Wrinkled seeds, yellow and green cotyledons, purple and white flowers, inflated and constricted ripe pods, green and yellow unripe pods, axial and terminal flowers, and tall and dwarf stems.

For the purpose of this paper we will take the case of cotyledon colour as a simple illustration of them all.

If an ordinary ripe pea seed be examined, it will be found to consist

of at least two distinct parts, viz. the seed-coat or skin which may be peeled off, and the cotyledons within. The two cotyledons are, of course, a part of the embryo plant, it will, therefore, be easily perceived that if the seed has been crossed, the cotyledons will partake of the nature of both parents, while on the other hand, the seed-coat or skin is a purely maternal character like the seed-pod itself.

The colour of the seed-coat may, therefore, be for the present ignored, and the cotyledon colour alone considered.

On this basis most pure races of peas may be divided into two classes, *yellow* and *green*.

Mendel crossed a pure yellow pea with pollen of a green pea, and the result was all yellow peas.

He then changed the sexes and crossed a green pea with pollen of a yellow pea, and the result was still all yellow peas. These experiments were repeated many times, and always with the same result. Mendel therefore concluded that pure yellow peas were dominant over pure green peas, and that the influence of the sexes was equal in heredity. Mendel then sowed these hybrid yellow peas of the first generation, and allowed the plants raised therefrom to fertilise themselves individually: each of these plants in the second generation bore seeds of the two colours, yellow and green, both colours being often found in the same pod. This proved that the hybrid yellow peas contained the green factor in a latent state. So that when the cross between pure yellow and green peas gave hybrid yellow peas, Mendel called the yellow character *dominant* over the green character, which he called *recessive*: the green character having receded in the first generation to re-appear in the second.

Mendel then tested the yellow and green peas obtained in the second generation. First, he sowed the green peas and allowed the plants to fertilise themselves individually, and *all produced green seeds* in the third generation. This experiment was repeated for six generations, and all still produced green peas with no trace of the dominant yellow ancestry.

Here Mendel made his most important discovery. Many earlier experimenters found that the offspring of hybrids resembled their grandparents as these green peas did, but Mendel alone carried on the experiment for several generations to see if they bred true, and he found that they did. These green peas therefore were pure green with no taint of yellow notwithstanding that both parents and two grandparents were dominant yellow.

Mendel next tested the yellow peas of the second generation by self-fertilisation, and he found them to be of two kinds—pure yellow and hybrid yellow. The pure yellow peas grew into plants which bore all yellow seeds, while the hybrid yellow peas produced plants each bearing a mixture of yellow and green peas, often in the same pod, just as their own parents did. The pure yellow peas remained fixed and bred true to type for the six generations in which they were tested, while the hybrid yellow peas gave pure yellow, hybrid yellow, and pure green peas, as their parents did.

Throughout the experiments the pure yellow peas were quite indistinguishable from the hybrid yellow, and their true nature could only be determined by their behaviour when bred from.

To sum up the experiments we find that pure yellow crossed with pure green gave all hybrid yellow peas. These hybrid yellow peas, self-fertilised, gave three distinct types, viz.:—pure yellow, hybrid yellow, and pure green.

This purity of the extracted yellow dominants, and of the extracted green recessives, was quite unsuspected, and forms the basis of the Mendelian principles of heredity. Further, Mendel found that the above three types always appeared in certain definite proportions, viz.:—1 pure yellow : 2 hybrid yellow : 1 pure green. For instance, in the second generation, out of 8023 seeds, there were 6022 yellow, and 2001 green, being practically a ratio of 3 yellow : 1 green, and out of 519 plants raised from these yellow seeds, 166 bore all yellow seeds, while 353 bore both yellow and green seeds mixed, *i.e.*, practically a ratio of 1 pure yellow : 2 hybrid yellow. So that the yellow and green seeds of the second generation really consisted on the average, of 1 pure yellow : 2 hybrid yellow : 1 pure green, *i.e.*, 25 per cent. pure yellow, 50 per cent. hybrid yellow, and 25 per cent. pure green.

It may be observed that although these average numbers and definite ratios are not at all essential to the conception of gametic purity, yet there is no doubt that it was by their suggestive aid that Mendel was able to formulate his principles of heredity. In Mendel's day it was known that each individual plant or animal developed from a single cell, and that this single cell was, as a rule, the result of the union of an egg-cell of the mother with a pollen or sperm cell of the father. Ordinary experience showed that a pure yellow pea self-fertilised produced yellow seeds, and similarly, a green pea produced green seeds. From this Mendel concluded that pure yellow peas gave

off egg-cells and pollen-cells which contained the necessary factor for producing the "yellow" character, and similarly that green peas gave off germ-cells which contained the factor of the "green" character.

It is interesting to note in passing that in so doing, Mendel clearly anticipated the later theories of Darwin (1868), Galton (1889), De Vries (1889), and Weismann (1893). On this hypothesis, when a pure yellow pea is self-fertilised, or pollinated with another pure yellow pea, the yellow factor Y in the egg-cell unites with the yellow factor Y in the pollen-cell, and gives rise to a pure yellow pea of constitution YY : in the same way a pure green pea self-fertilised gives rise to a pure green pea GG . When, therefore, a pure yellow pea is pollinated with a green pea, or *vice versa*, the yellow factor Y unites with the green factor G , giving rise to a hybrid yellow-green pea YG . Owing, however, to dominance of yellow over green in the development of the soma, the hybrid pea is yellow, though all the time, as its breeding proves, its germinal constitution is YG . Now we come to the most important part of the Mendelian hypothesis. Mendel conceived that *the factors Y and G which come together by conjugation in the hybrid YG , still retain their identity and individuality: and when the hybrid YG gives off gametes (i.e. germ-cells, either egg- or pollen-cells) the factors Y and G separate again, so that each gamete contains either the Y or the G factor, but not both.* On this hypothesis, the hybrid YG , on the average, gives off egg-cells $1 Y : 1 G$, i.e., 50 per cent., containing the yellow factor, and 50 per cent. the green factor. Similarly, the hybrid YG gives off pollen-cells $1 Y : 1 G$. So that YG , self-fertilised, as in Mendel's experiments, would, on the average, give the following gametic unions:—

$$1 Y \text{ ♀} + 1 Y \text{ ♂} = 1 YY.$$

$$\left. \begin{array}{l} 1 Y \text{ ♀} + 1 G \text{ ♂} \\ 1 G \text{ ♀} + 1 Y \text{ ♂} \end{array} \right\} = 2 YG.$$

$$1 G \text{ ♀} + 1 G \text{ ♂} = 1 GG.$$

The total offspring of YG , self-fertilised, would therefore on the average consist of $1 YY : 2 YG : 1 GG$, i.e., 25 per cent. pure yellow, 50 per cent. hybrid yellow, and 25 per cent. pure green. This ratio calculated on Mendel's hypothesis of gametic purity is practically identical with the ratio actually observed by Mendel in his experiments, as shown before. The simple idea of the purity of the germ-cells—or gametic purity, as it is now called—is the most important of Mendel's discoveries, and on it are founded all the complicated calculations of the probabilities of heredity in different individual matings.

As an illustration of this we will take a simple combination of two characters in Peas, viz.:—seed-shape and seed-colour. Given the mating of pure round yellow with wrinkled green, what may be expected in the first, second, and succeeding generations on the basis of Mendel's law of gametic purity and his experience as to dominance?

In the first generation all the hybrids seeds will be round yellow, whichever way the cross is made, because, as Mendel found, the round and yellow characters are as a rule dominant over the corresponding wrinkled and green characters which are recessive.

Mendel's experiments gave all round yellow peas in this cross. My own experiments were with the same characters differently coupled, Mendel's being round yellow \times wrinkled green, and mine wrinkled yellow \times round green. The results in both cases were the same, all the hybrid seeds being round yellow, showing that the dominance of round over wrinkled, and yellow over green, is the peculiar property of the character itself, and is quite independent of the manner of mating. In the second generation these round yellow hybrids, self-fertilised, will produce, on the average, a proportion of 3 R : 1 W, and 3 Y : 1 G; and, taking the two characters in combination, there will be, on the average, 9 RY : 3 RG : 3 WY : 1 WG. Mendel's original experiments gave, out of 556 seeds, 315 RY : 108 RG : 101 WY : 32 WG, which is close to the calculated expectation for 560 seeds, which is 315 RY : 105 RG : 105 WY : 35 WG. My own experiments have given, out of 1755 seeds, 997 RY : 338 RG : 313 WY : 107 WG, which is close to the calculated expectation for 1760 seeds, which is

$$990 \text{ RY} : 330 \text{ RG} : 330 \text{ WY} : 110 \text{ WG}.$$

In the third generation, the four types, RY, RG, WY, and WG, of the second generation, self-fertilised, will give the following results:—

(1) The WG seeds will breed true, producing plants, all of which will bear only wrinkled green peas.

(2) The WY seeds will produce two kinds of plants, of which, on the average, one plant in three will breed true, bearing all wrinkled yellow seeds,—the remaining two plants bearing wrinkled yellow and wrinkled green seeds mixed, in the average proportion of 3 WY : 1 WG.

(3) The RG seeds will also produce two kinds of plants, of which, on the average, one plant in three will breed true, bearing all round green seeds, the remaining two plants bearing round green and wrinkled green seeds mixed, in the average proportion of 3 RG : 1 WG.

(4) The RY seeds will produce four kinds of plants, of which, on

the average, one plant in nine will breed true, bearing all round yellow seeds; two plants in nine will bear round yellow and wrinkled yellow seeds mixed in the average proportion of 3 RY : 1 WY; two plants in nine will bear round yellow and round green seeds mixed in the average proportion of 3 RY : 1 RG, while the remaining four plants in nine will bear round yellow, round green, wrinkled yellow, and wrinkled green seeds mixed, in the average proportion of 9 RY : 3 RG : 3 WY : 1 WG.

All these complicated anticipations, easily calculated on the basis of Mendel's law, were practically realised, and proved in Mendel's original experiments.

In my own experiments, recently harvested, out of 115 individual plants of the four types tested—bearing, in all, over 6000 seeds—I have not met with a single exception to the Mendelian conception of gametic purity, and the seed numbers are all very close to the Mendelian expectation. Indeed, when we come to consider the peculiar nature of the gametes, and the various vicissitudes to which they must be liable, both in formation and distribution, it is really surprising that the numbers work out as closely as they do.

In the fourth and succeeding generations the *pure* RY, RG, WY, and WG types will continue to breed true, being in fact permanently fixed on their first appearance, notwithstanding their mixed ancestry, and these will remain constant to type under self-fertilisation until a mutation arises, or may be some accidental cross is effected. Mendel tested the purity of these extracted races through six generations, and in the case of the WY race, known as *British Queen*, used in my experiments, which appears to have been originally extracted by Knight from his crosses in 1787, the WY characters have continued to breed true for more than a hundred generations.

In the fourth and succeeding generations the hybrid RY, RG, and WY types will behave precisely the same as they did in the third generation, splitting up into pure and hybrid forms again in the same average proportions. Mendel tested these also through six generations.

The production of four types in all these experiments, viz., RY, RG, WY, and WG, shows that all the possible combinations of R and W seed-shape with Y and G seed-colour, have been effected, and that, therefore, seed-shape and seed-colour are two distinct characters, each being inherited or transmitted independently of the other. If it were not so, and the two characters, shape and colour, were correlated and inherited as one character, then only two types would have occurred in

both Mendel's and my own experiments. In Mendel's experiments the two types would have been RY and WG, and in mine, WY and RG.

But as we have seen both experiments gave all the four possible types, so that it is clear that seed-shape and seed-colour are distinct characters with an independent inheritance. Mendel's discovery of this elementary fact was one of the secrets of his success, and his experimental demonstration of the existence of single heritable characters proved once and for all that *the true unit of heredity is not the individual, but the single character*.

So far as Peas are concerned Mendel's results have been fully confirmed by the experiments of Correns, Tschermak, Bateson, and the writer. The question naturally arises as to how far Mendel's law applies to plants other than Peas.

Though barely four years have passed away since Mendel's discoveries were made known, the progress already made is really remarkable. First and foremost we have the experiments of De Vries, which show that Mendel's law applies to many different genera of garden plants, including *Amarantus*, *Oenothera*, *Linaria*, *Antirrhinum*, *Papaver*, *Aster*, *Chrysanthemum*, *Veronica*, *Viola*, *Chelidonium*, *Agrostemma*, *Hyoscyamus*, *Clarkia*, *Silene*, *Lychnis*, *Trifolium*, *Solanum*, *Calliopsis*, *Datura*, &c., as well as to Maize. Next, we have the experiments of Correns with Stocks (*Matthiola*), Maize (*Zea*), and *Mirabilis*, then those of Tschermak with Stocks, and Beans (*Phaseolus*). Afterwards, we have the significant experiments of Bateson and Saunders with Stocks, *Lychnis*, *Datura*, *Atropa*, *Solanum*, *Primula*, and Sweet Peas (*Lathyrus*). The experiments of Spillman and Biffen with Wheat; Emerson with Beans; Wilson with Oats, and the writer with Orchids (*Paphiopedilum*), *Berberis*, *Primula*, and Sweet Peas. So far as plants are concerned, it is evident that Mendel's law applies to a large number of characters in many genera and species belonging to various natural orders, and it seems likely that in course of time, Mendel's law will be found to apply to plants generally. The interesting question now arises as to how far Mendel's law applies to animals (including Man), as well as plants.

Cuénot, in his experiments with fancy Mice in 1902, was, apparently, the first to apply Mendel's law to animals with results of great value; then Bateson, in his important experiments with Poultry, and his application of the Mendelian principles to the earlier experiments of others with fancy Rats, Mice, Canaries, Pigeons, Cattle, and Goats. Afterwards, we have the experiments of Castle and Allen with Guinea-

pigs, Mice, and Rabbits; those of Darbshire with Mice; Woods with Rabbits; Davenport with Mice; and the writer with Poultry and Rabbits. With regard to the application of the Mendelian principles to Man, the experimental method used with such success in plants and domestic animals is obviously not available, but some interesting observations have been made by Castle and Farabee with regard to the heredity of negro albinism, by Garrod and Weldon on albinism in Sicily, and by Davenport on the heredity of polydactylism, which, though necessarily inconclusive, owing to the lack of precise data, yet seem to point towards a Mendelian interpretation.

Space will not allow any reference to the interesting details of the various experiments with plants and animals noted above, but the list of authors and subjects given below will enable the reader to refer to the original papers, all of which will repay careful study.

In conclusion, the writer gives a brief list of some of the Mendelian characters that he has found in his own experiments with plants and animals. The alternative characters of each subject are arranged in pairs, the first-named of the pair being usually the dominant one, the other being recessive.

In many cases, however, the dominance is incomplete, the influence of the recessive character being apparent in the soma of the hybrid in varying degrees: in some cases the hybrid characters are quite intermediate, and in a few cases characters appear that are not visible in either parent, being apparently reversionary. Nevertheless, with few exceptions, the characters appear to segregate in accordance with the Mendelian principles of gametic purity.

PEAS (*Pisum sativum*): Round and wrinkled seeds: yellow and green cotyledons.

ORCHIDS (*Paphiopedilum* (*Cypripedium*) *insigne*, *P. Spicerianum*, and *P. Boxallii*): "white" and "green," spotted and clear, blotched and clear, spotted and blotched, barred and clear, dorsal sepal; also eight pollinia (*Lælia*), and four pollinia (*Cattleya*).

BERBERIS (*B. Darwinii* and *B. empetrifolia*): Hairy and glabrous stems: 3 spines and 5 spines: glaucous and green leaves, revolute, and flat leaves.

SWEET PEAS (*Lathyrus odoratus*): Tall and dwarf (*Cupid*) stems: Red Bicolor (Painted Lady) and White, Maroon (Black Knight) and White, Maroon and Red Bicolor flowers.

PRIMULA (*P. sinensis*): Palm-leaved and fern-leaved.

POULTRY (White Leghorn, Black Hamburg, Houdan, and Buff

Cochin): White and black, black and buff, white and buff down and plumage: rose and single, rose and leaf, leaf and single combs: extra-toe and normal feet: feathered and clear shanks, white and yellow shanks, blue and yellow shanks: crested and clear head.

RABBITS (White Angora, Belgian Hare, Black Dutch): Pigmented and albino skin and coat (with which are correlated dark and pink eyes, normal and swaying habit): grey and black coat, brown and black coat: normal fur and Angora wool: self-coloured and Dutch-marked coat.

LIST OF AUTHORS AND SUBJECTS.

- ALLEN, G. M. (1904). The Heredity of Coat-color in mice. *Proc. Amer. Acad. Arts and Sci.* XL. pp. 61-163.
- BATESON, W. (1902). Mendel's Principles of Heredity. (Cambridge University Press.) 212 pp.
- (1903). The present state of knowledge of colour-heredity in Mice and Rats. *Proc. Zool. Soc. Lond.* II. pp. 71-99.
- (1904). Heredity and Variation in *Primula sinensis*. *Linn. Soc. Lond.* 18th Feb.: abstract in *Gard. Chron.* 1904, I. p. 143.
- BATESON, W., AND SAUNDERS, E. R. (1902). Experimental studies in the Physiology of Heredity. *Reports to Evol. Com. Roy. Soc. Lond.* I. 160 pp.
- BIFFEN, R. H. (1903). Experiments on Wheat. *Nature*, LXIX. pp. 92-3.
- (1904). Mendel's Laws, and their application to Wheat hybrids. *Linn. Soc. Lond.* 18th February: abstract in *Gard. Chron.* 1904, I. p. 143.
- BOND, C. J. (1899). Experiments bearing on the question of the inheritance of one group of acquired characters in Plants and Animals. *Trans. Leicester Lit. and Phil. Soc.* V. 12 pp.
- CASTLE, W. E. (1903). (a) Mendel's Law of Heredity. *Science*, XVIII. pp. 396-406.
- (1903). (b) The Heredity of Angora coat in Mammals. *Science*, XVIII. pp. 760-1.
- CASTLE, W. E., AND ALLEN, G. M. (1903). The Heredity of Albinism. *Proc. Amer. Acad. Arts and Sci.* XXXVIII. pp. 603-622.
- CASTLE, W. E., AND FARABEE, W. C. (1903). Notes on negro albinism. *Science*, XVII. pp. 75-6.
- CORRENS, C. (1900). (a) G. Mendel's Regel über das Verhalten der Nachkommen-schaft der Rassenbastarde. *Ber. deut. bot. Ges.* XVIII. pp. 158-168.
- (1900). (b) Gregor Mendel's Versuche über Pflanzen-Hybriden und die Bestätigung ihrer Ergebnisse durch die neuesten Untersuchungen. *Bot. Zeit.* LVIII. p. 229.
- (1900). (c) Ueber Levkojen-Bastarde zur Kenntniss der Grenzen der Mendel'schen Regeln. *Bot. Centr.* LXXXIV. p. 97.
- (1901). (a) Ueber Bastarde zwischen Rassen von Zea Mays. *Ber. deut. bot. Ges.* XIX. p. 211.
- (1901). (b) Bastarde zwischen Maisrassen. *Bibliotheca Botanica.* Heft, 53.
- (1903). Ueber Bastardirungs-Versuche mit *Mirabilis*-Sippen. *Ber. deut. bot. Ges.* XX. pp. 594-608.

- CUENOT, L. (1902). La loi de Mendel et l'Hérédité de la pigmentation chez les Souris. *Arch. Zool. exp.* x. Notes et Revue. pp. 27-30.
- (1903). (a) La loi de Mendel et l'Hérédité de la pigmentation chez les Souris. *Compt. Rend. Paris*, CXXXIV. pp. 779-781.
- (1903). (b) L'Hérédité de la pigmentation chez les Souris. (2me. Note.) *Arch. Zool. exp.* i. Notes et Revue. pp. 33-41.
- (1904). L'Hérédité de la pigmentation chez les Souris. (3me. Note.) *Arch. Zool. exp.* II. Notes et Revue. pp. 45-56.
- DARBISHIRE, A. D. (1904). (a) On the result of crossing Japanese Waltzing with Albino Mice. *Biometrika*, III. pp. 1-51.
- (1904). (b) On the bearing of Mendelian Principles of Heredity on current theories of the Origin of Species. *Mem. and Proc., Manchester Lit. and Phil. Soc.* XLVIII. pp. 1-19.
- DARWIN, C. (1868). Animals and Plants under Domestication. 2 vols. (2nd ed. 1893) (Murray).
- DAVENPORT, C. B. (1904). (a) Colour Inheritance in Mice. *Science*, XIX. pp. 110-114.
- (1904). (b) Wonder Horses and Mendelism (contains notes on Heredity of polydactylism and deaf-mutism in Man). *Science*, XIX. pp. 151-153.
- EMERSON, R. A. (1902). Preliminary Account of Variation in Bean Hybrids. *15th Report, U.S. Expt. St.* Nebraska. pp. 30-43.
- FOCKE, W. O. (1881). Die Pflanzen-Mischlinge. (Bornträger, Berlin.) 569 pp.
- GALTON, F. (1898). Natural Inheritance. (Macmillan.) 259 pp.
- HURST, C. C. (1898). Notes on some Curiosities of Orchid Breeding. *Journ. Roy. Hort. Soc. Lond.* XXI. pp. 442-486. (Also *Nature*, LIX. pp. 178-181.)
- (1900). Experiments in Hybridisation and Cross-Breeding. (1st Int. Conf. Hyb. Lond. 1889.) *Ibid.* XXIV. pp. 90-126.
- (1902). Mendel's Law applied to Orchid Hybrids. (1st Note.) *Ibid.* XXVI. pp. 688-695.
- (1903). (a) Mendel's Methods of Plant Breeding. (2nd Int. Conf. Hyb. New York, 1902.) *Gard. Chron.* 1903, I. pp. 33-34 and 76.
- (1903). (b) Mendel's Principles applied to Orchid Hybrids. (2nd Note.) *Journ. Roy. Hort. Soc. Lond.* XXVII. pp. 614-624.
- (1903). (c) Mendel's Principles applied to Wheat Hybrids. *Ibid.* XXVII. pp. 876-893. (Contains SPILLMAN (1902) (a).)
- (1903). (d) Recent Experiments in the Hybridisation of Orchids. (Sect. K, Brit. Assoc. Southport, 1903.) *Gard. Chron.* 1903, II. pp. 226-7.
- (1904). (a) Experiments in the Heredity of Peas. *Journ. Roy. Hort. Soc. Lond.* XXVIII. pp. 483-494.
- (1904). (b) Experiments on Heredity in Rabbits. (Sect. D, Brit. Assoc. Cambridge, 1904.) Abstract in *Nature*, LXX. pp. 538-9.
- KNIGHT, T. A. (1799). An Account of some Experiments on the Fecundation of Vegetables. *Phil. Trans. Roy. Soc. Lond.* II. p. 195.
- MENDEL, G. J. (1865). Versuche über Pflanzen-Hybriden. *Verh. naturf. Ver. Brünn*, IV. (Abh.), 47 pp. Reprinted in *Flora*, 1901, and in Ostwald's *Klassiker d. exakten Wiss.* English translation by Bateson in *Journ. Roy. Hort. Soc. Lond.* 1901, XXVI. pp. 1-32, and in BATESON (1902).

- MENDEL, G. J. (1869). Ueber einige aus künstlicher Befruchtung gewonnenen *Hieracium*-Bastarde. *Ibid.* VIII. (Abh.), p. 26. (English translation in BATESON, 1902.)
- PEARSON, K. (1904). Mathematical contributions to the theory of Evolution, XII. On a generalised theory of Alternative Inheritance with special reference to Mendel's Laws. *Phil. Trans. Roy. Soc. Lond.* CCIII. pp. 53-86.
- SPILLMAN, W. J. (1902). (a) Quantitative Studies on the Transmission of Parental Characters to Hybrid Offspring. (Ann. Conv. Expt. St. 1901.) *U.S. Dept. Agric. Expt. St. Bull.* 115, 1902, pp. 88-98.
- (1902). (b) Exceptions to Mendel's Law. *Science*, XVI. pp. 794-796.
- TSCHERMAK, E. (1900). Ueber künstliche Kreuzung bei *Pisum sativum*. *Zeitschrift. f. d. landwirtsch. Versuchswesen in Oesterr.* III. pp. 465-555.
- (1901). (a) Weitere Beiträge über Verschiedenwerthigkeit der Merkmale bei Kreuzung von Erbsen und Bohnen. *Ibid.* IV. p. 641.
- (1901). (b) Ueber Züchtung neuer Getreiderassen mittelst künstlicher Kreuzung. *Ibid.* IV. p. 1029.
- (1902). Dei gegenwärtige Stand der Mendel'schen Lehre und die Arbeiten von W. Bateson. *Ibid.* 1902, 106 pp.
- (1903). Die Theorie der Kryptomerie und des Kryptohybridismus. *Beihfte z. bot. Centr.* XVI. 25 pp.
- (1904). Weitere Kreuzungsstudien an Erbsen. Levkojen und Bohnen. *Zeitschrift. f. d. landw. Versuchswesen in Oesterr.* 1904, 106 pp.
- VRIES, H. DE (1889). Intracellulare Pangenesis. (Jena.)
- (1900). (a) Sur la loi de disjonction des hybrides. *Compt. Rend. Acad. Sci. Paris*, CXXX. pp. 845-7.
- (1900). (b) Das Spaltungsgesetz der Bastarde. *Ber. deut. bot. Ges.* XVIII. pp. 83-90. (English translation in *Journ. Roy. Hort. Soc. Lond.* 1901, XXV. pp. 243-248.)
- (1900). (c) Ueber erbungleiche Kreuzungen. *Ibid.* XVIII. pp. 435-443. (English translation in *Journ. Roy. Hort. Soc.* 1901, XXV. pp. 249-255.)
- (1900). (d) Sur les Unités des caractères spécifiques et leur application à l'étude des hybrides. *Rev. Gén. Bot.* XII. p. 257. (English abstract in *Gard. Chron.* 1900, II. pp. 391-2, and 432.)
- (1903). Die Mutations-Theorie (Elementare Bastardlehre). II. (Veit, Leipzig.)
- WEISMANN, A. (1893). The Germ-Plasm, a Theory of Heredity. (English translation Cont. Sci. Ser., Walter Scott, London.)
- WELDON, W. F. R. (1902). Mendel's Laws of Alternative Inheritance in Peas. *Biometrika*, I. pp. 228-254.
- (1904). Albinism in Sicily and Mendel's Laws. *Ibid.* III. pp. 107-109.
- WILSON, J. H. (1904). Variation in Oat Hybrids. *Nature*, LXIX. p. 413.
- WOODS, F. A. (1903). Mendel's Laws and some records in Rabbit Breeding. *Biometrika*, II. pp. 299-306.

X

EXPERIMENTS IN THE HEREDITY OF PEAS¹

The following is a preliminary account of a series of experiments commenced in 1902 with garden Peas (*Pisum sativum*). The primary object was to repeat Mendel's original experiments as closely as possible, and test his principles of heredity. (Mendel 1865, Bateson 1901.) The secondary object was to endeavour to ascertain more fully the precise nature of Mendel's categories of seed shape and cotyledon colour in Peas. (Cf. Weldon 1902.)

SEED SHAPE.

For many years it has been the custom in gardens to divide the ordinary races of white-flowered Peas into two classes, "Round" and "Wrinkled." In the "Round" class are included all those with round, roundish, or rounded seeds, the surface of the seeds being either quite smooth or slightly pitted. In the "Wrinkled" class are included all those with angular, squared, or flattened seeds, the surface of the seeds being deeply dented, broadly wrinkled, or shrivelled. The precise nature of wrinkling in Peas does not yet appear to have been determined, but Mr Bateson cites the analogous case of Round and Wrinkled Maize, in which the "Round seeds contain much unconverted starch, while in the Wrinkled or Sugar-maize this seems to be converted in great measure as the seed ripens; with the result that on drying the walls collapse. In such seeds we may perhaps suppose that the process of conversion, which in round seeds takes place on germination, is begun earlier, and perhaps the variation essentially consists in the premature appearance of the converting ferment." (1902, p. 123.)

Mr Bateson proceeds to say that it would be rash to suggest that such a process may be operating in the Pea; but when we consider that wrinkled Peas are usually sweeter than round ones and will not ger-

¹ Reprinted from the *Journal of the Royal Horticultural Society*, xxviii. Parts 3 and 4, pp. 483-494 (1904).

minate so well as round ones if sown too early, and in a dry state do not retain their vitality so long as round ones, it seems probable that the nature of wrinkling in Maize and Peas may not only be analogous but identical. It is to be hoped that the chemists will take the matter up and ascertain the precise nature of Round and Wrinkled Peas. In carrying out my experiments I have been much impressed by the observation of the powerful influence of the conditions of life on seed shape in Peas, and though my evidence is not yet complete, I think that there is no doubt that some, at all events, of the angularity, squareness, flattened sides and deep dents are directly caused by the pressure of the Peas against one another in the pod, and also by the constriction of the pod itself. I find that, as a rule, the roundest Peas are small, or have plenty of room in the pod, while the most wrinkled Peas are large or are tightly packed in the pod. It seems likely, therefore, that a great deal of irregularity in shape, found in certain races with large round seeds, may be directly due to the struggle for growth among the Peas within the pod, altogether in spite of the hereditary tendency to roundness. In the majority of races, the two classes "Round" and "Wrinkled" are distinctly discontinuous, and breed true to type when self-fertilised, so that it is hardly possible to confuse one type with another. In some cases, however, as Professor Weldon has carefully pointed out, there is a considerable range of variation both in the "Round" and "Wrinkled" classes, forming in a few cases an almost continuous series between the two (1902, pl. II.), and Mr Bateson even goes so far as to suggest that some races are normally intermediate in shape (1902, p. 123). Professor Weldon admirably sums up the ordinary discontinuous nature of the "Round" and "Wrinkled" categories, as follows: "The categories are undoubtedly often discontinuous, the most wrinkled seed of such a (round) race as 'Empress' or 'Victoria' being so much smoother and more rounded than the most regular seed of the typically 'wrinkled' races that no one who knows both races would hesitate for a moment in deciding which race a given seed resembled." (1902, p. 236.) We may therefore safely say, that in regard to seed shape at all events, Mendel's categories of "Round" and "Wrinkled" ("angular") are distinct and unambiguous. In selecting the "Round" and "Wrinkled" races for my own experiments, I thought it would perhaps simplify matters still more if I selected, for the first experiment, two races which showed but little variation in seed shape. For the "Round" race I chose 'Harrison's Early Eclipse,' and for the "Wrinkled," 'British Queen.'

Both races have been intimately known to me for twenty years, and I have always found them reliable in their respective characters. Messrs Harrison & Sons of Leicester kindly inform me that their 'Eclipse' was originally a selection from the round blue-seeded 'Harbinger' introduced by Laxton early in the seventies. Mr N. N. Sherwood, in his useful and interesting paper on Garden Peas in this *Journal*, states that 'British Queen' is a direct descendant of 'Knight's Tall Wrinkled Marrow' (1899, p. 251), which was apparently obtained by Knight (that famous experimenter in horticulture, and former President of the Royal Horticultural Society) from his numerous crossings between white and purple-flowered Peas in 1787. Though the details of Knight's experiments are not altogether clear (1799, p. 195), yet it is interesting to note that in many respects they plainly anticipated Mendel's own results. For instance, in the dominance of tall habit over dwarf, purple flowers over white, and "grey" (brown) seed coats over white; also in the immediate fixing of the tall dominants and the white-flowered and white-coated recessives, both by self-fertilisation ("simple culture") of the tall purple-flowered and grey-coated hybrids, as well as by recrossing with one of the parent forms. Previous to Mendel's discoveries being made known, Knight's experiments with Peas were practically unintelligible, but now, in the light of Mendel, they appear quite obvious. There is no doubt as to the antiquity of the 'British Queen' race, otherwise known as 'Knight's Tall Wrinkled Marrow,' and if it originated from Knight's crosses in 1787 it provides an interesting illustration of the vigorous persistence of a race after more than a hundred generations of close inbreeding by self-fertilisation.

In order to simplify the experiments still more, I selected sub-races of both 'Eclipse' and 'British Queen' as follows:

I first selected individual seeds of 'Eclipse' which were apparently perfectly round and smooth (save, of course, for the slight suture or seam at the base of the seed); to be precise, all these seeds were rounder than Professor Weldon's roundest Peas of Lightning (1902, pl. II., fig. 13), and equally smooth. These seeds were sown and produced plants which gave precisely similar seeds, perfectly round and smooth, with no trace of irregularity or pitting. This apparently constant sub-race of 'Eclipse' produced the parent plants used in the experiments.

In the same way a sub-race of the most wrinkled 'British Queen' was selected. Individual seeds were chosen which were all angular,

flattened, deeply-dented, and broadly wrinkled, without a trace of either roundness or smoothness; these may be compared to Professor Weldon's most wrinkled Peas of 'Telephone' (1902, pl. II., fig. 6). These seeds were sown and produced plants which gave similar seeds. This apparently constant sub-race of 'British Queen' produced the parent plants used in the experiments.

First Generation (F₁).

EXPERIMENT 1.—'British Queen' ♀ × 'Eclipse' ♂
(Wrinkled ♀ × Round ♂).

A specimen plant of 'British Queen' was selected as the seed parent, and as soon as the first flower-buds appeared, the sepals, standard, wings, keel, and immature stamens were all cleanly removed at an early stage, and at the same time the ripe pollen of a partially-expanded flower of an individual plant of 'Eclipse' was applied in profusion, completely covering the susceptible surface of the pistil. In a few days the pods began to form and ultimately 19 hybrid seeds were developed, all of which were round when dried, thus demonstrating once more the dominance of round seeds over wrinkled, and confirming the previous experiments of Mendel (1865), Correns (1900), Tschermak (1900-1901), and Bateson (1902). These dominant hybrid Peas, though technically round, were slightly imperfect in their roundness, all being practically the same shape. They may be described as rounded, with slightly elongated apex, and rather flattened sides; all were practically smooth with faint traces here and there of both slight pitting and feeble wrinkling; they compare well with Professor Weldon's 'Telegraph' (1902, pl. II., fig. 2A), except that their surface is much smoother. There is not yet sufficient evidence to show whether these slight imperfections of roundness are due to the conditions of life or to incomplete dominance, or both, but so far the evidence seems to point towards the former rather than the latter, as all the Peas were large and were packed tightly in the pods, and it is indeed difficult to imagine how any of them could have been perfectly round under these conditions, whatever the hereditary tendency might have been.

This shows the necessity for caution in ascribing irregularities of seed shape to failure of dominance without first eliminating the influence of the conditions of life. It is obvious that size and weight, when considered as attributes in heredity, must necessarily be unreliable amid the changing conditions of life, yet it may be noted, with all due reservation, that in the parent seeds 6 of the largest 'British Queen'

just balanced 16 of the largest 'Eclipse,' while 5 of the largest hybrid seeds balanced the same 16 'Eclipse.' As size and weight appear to correspond fairly in seed Peas, this suggests that in hybrid Peas size is a purely maternal character, unlike shape, which is a hybrid character. Professor Correns has arrived at a similar conclusion in regard to the size of hybrid seeds of Maize (1901).

Second Generation (F₂).

DR × DR.

In 1903, 14 of the dominant round hybrids raised in Experiment 1 were duly sown: these produced 12 hybrid plants which, self-fertilised, gave 1755 seeds in the second generation. These seeds were distinctly of two types, round and wrinkled, both types being often produced in the same pod; some pods contained all round, but none contained all wrinkled.

The following is a list of the numbers of each type produced by the 12 individual plants:

		D	R
	Expt.	Round	Wrinkled
	2	27	6
	3	32	4
	4	24	11
	5	378	125
	6	15	5
	7	135	36
	8	62	12
	9	203	52
	10	287	107
	11	85	30
	12	72	25
	13	15	7
Total	1335	420
Actual ratio	3·1 D	: 1 R
Mendelian ratio	...	3 D	: 1 R

Out of the 1755 seeds of the second generation 1335 were round dominants, and 420 were wrinkled recessives, giving a ratio of 3·1 D : 1 R, which is close to the 3 : 1 expected by Mendel's law. It will be observed that in individual plants where the numbers are few the ratios fluctuate considerably, but where the numbers are 100 and over the ratios are on the whole fairly constant. This shows the necessity of dealing with large numbers in all quantitative experiments in heredity, otherwise the ratios will be irregular. On the other hand, a few numbers will suffice

for qualitative experiments, as may be seen in the above experiments; a dozen seeds would generally be sufficient to secure both the dominant and recessive types. With regard to the precise nature of the dominant and recessive characters in the second generation, no appreciable difference can be perceived in the respective seeds of the different experiments, so that we will take the seeds of Experiment 5 to represent them all.

The wrinkled recessives in Experiment 5 are practically indistinguishable from the seeds of the pure recessive grand-parent 'British Queen,' so far as shape is concerned; all are angular, squared, flattened, with deep dents and broad wrinkles.

The Round dominants in Experiment 5 are all unmistakably round, with no intermediate forms tending towards the wrinkled recessives: they are, however, slightly variable in their roundness and smoothness. For convenience they may be divided into three groups, though, as a matter of fact, the groups are almost continuous.

In order to enable others to identify and gain a clear idea of these three groups, I have compared them as closely as possible with Professor Weldon's photographs of seed shapes in Peas (1902, pl. II., figs. 1-18), and in quoting the figures by number, where there are two Peas in Professor Weldon's groups, I will term them respectively A and B, reading from left to right, in the same direction as the numbers.

Out of 100 full-sized round seeds raised in Experiment 5, 9 may be referred for shape alone to fig. 2A, and for smoothness alone to fig. 1B, all being nearly round and perfectly smooth: 72 may be referred to fig. 2A for both shape and pitting, though in all, the pitting is less extensive and pronounced: the remaining 19 may be referred to fig. 2B, being slightly irregular in shape, with shallow dents. It will be noted that 72 per cent. of the dominants of the second generation are similar to the dominant hybrids of the first generation, while the rest comprise a small percentage, varying on either side of the majority, and it seems probable that, if 100 seeds of the first generation could have been compared together (instead of the 19 actually compared), all these three types would have been found in the same proportions as in the second generation. In any case it seems likely that the slight imperfections of roundness and smoothness in both generations are due to the action of similar causes. That one of these causes is *not* the influence of the recessive character (causing incomplete dominance) is suggested by the fact that none of the dominants in the second generation are exactly like the pure dominants, and yet by Mendel's law one-third of them should be pure dominants; so that altogether it appears fairly

clear that in both the first and second generations the imperfections of roundness and smoothness are in some measure due to the conditions of life rather than to heredity. It was further observed that the 9 per cent. perfectly smooth seeds in the second generation were all smaller in size than the others, and the 19 per cent. which were the most irregular were the largest seeds of all; evidently, therefore, size is also a factor to be considered, and it is hoped that an examination of the third generation will determine this difficult and complicated question.

With regard to the size of the seeds of the second generation, they are sensibly smaller than those of the first generation. As a matter of fact, if the size of the seeds is a purely maternal character, as it certainly appeared to be in the former generation, then in this generation it should behave really as a first hybrid character, say intermediate between the size of 'British Queen' and 'Eclipse.' Judging, as before, the size by the weight, I found that six of the largest 'British Queen' seeds just balanced sixteen of the largest 'Eclipse,' while in these hybrids I find that it takes eight of the largest seeds to balance either the six 'British Queen' or the sixteen 'Eclipse.' If the hybrid seeds were exactly intermediate between the parents, the ordinary mean would be 11, so that broadly speaking the hybrid size favours the 'British Queen' parent slightly more than the 'Eclipse.' But there are other complications which may possibly account for this departure from the mean; for instance, all these hybrid seeds were borne on extraordinarily vigorous hybrid plants seven to eight feet high, in which the tall 6½-feet 'British Queen' parent was distinctly dominant over the dwarfer 2½-feet 'Eclipse' parent, thus again confirming Mendel's experience, in which the tall character was always dominant over the short character.

This was the case with all my twelve hybrids (Experiments 2-13), and, just as Mendel found, the dominant hybrids exceeded in height and vigour the pure dominant parent (Mendel 1865, Bateson 1901). It seems reasonable to suppose that such extra vigour in the hybrids would affect the size of the seeds borne thereon. It may also be worthy of note that the flowers of the hybrids (Experiments 2-13) were precisely similar to those of the 'British Queen,' having the large, substantial, pure white flowers of that parent, with no trace of the small, semi-transparent, greenish-white flowers of the 'Eclipse.'

These comparisons were made at the same time, all the plants, hybrids and parent races, being grown side by side in similar soil, being practically under the same conditions of life.

COTYLEDON COLOUR.

Although seed shape in Peas depends on the shape of the cotyledons, it can be easily determined without removing the seed-coat or outer skin. On the other hand, in some races the cotyledon colour is masked by the more or less thick and pigmented seed-coat.

In gardens, it is customary to divide ordinary Peas into "green," "white," and "blue." The "white" Peas have usually yellow cotyledons, and the "green" ones green cotyledons; but in some cases "green" varieties with a thick green skin have yellow cotyledons: "blue" Peas have usually green cotyledons seen through a semi-transparent skin. It is, therefore, not at all safe to judge the cotyledon colour in all races by the outward appearance of the seed; and in order to determine the cotyledon colour in the thick-skinned races, the seed-coat has to be removed.

If this be done entirely the germination of the seed is naturally affected, so that in these experiments it was thought desirable to select races whose seed-coats were more or less transparent. In 'British Queen' we have a "white" seed with yellow cotyledons obscurely seen through a white seed-coat; in 'Eclipse' we have a "blue" seed with green cotyledons more clearly seen through a white seed-coat. In both cases the seed-coat is more or less transparent, the skin being rather thicker in the former than in the latter; in both cases, too, the white seed-coats themselves contain varying amounts of green pigment when the seeds are not well ripened, and if the seeds are gathered prematurely this green pigment persists. Great care is, therefore, necessary in dealing with these complications in seed-coat colour, and the whole question bristles with difficulties owing to the changing conditions of life. When we come to deal with the heredity of cotyledon colour, the necessity of carefully eliminating the question of seed-coat colour becomes even more evident. There is a vital difference between the hereditary nature of cotyledon colour and that of seed-coat colour, inasmuch as the cotyledons, representing as they do the first two leaves of the hybrid plant, are hybrid in their nature, partaking of the qualities of both parents, while on the other hand the seed-coat is purely a maternal structure, so that it is possible to have two distinct generations present in one seed. For example, in Experiment 1, where a plant of 'British Queen' was fertilised with pollen of 'Eclipse' in the summer of 1902, the ripe seeds resulting from that cross, gathered in the autumn of the same year, were true hybrids of the first generation, so far as the shape and

colour of the cotyledons were concerned, but the seed-coats of the hybrid Peas were purely maternal, *i.e.* 'British Queen,' being as much a part of the mother plant as the pods. When the hybrid seeds were sown in 1903, and grew into hybrid plants of the first generation in the same summer, they were allowed to self-fertilise, and the resulting seeds, gathered in the same autumn, were, so far as seed shape and cotyledon colour were concerned, hybrid seeds of the second generation (Experiments 2-13); but the seed-coats of these same seeds were maternal, *i.e.* hybrids of the first generation; and so on with all the generations. It is true that, occasionally, the foreign pollen does apparently influence the maternal seed-coat and even the pod, and Darwin (1868, p. 428) has collected a number of such cases from the experiments of Gärtner, Berkeley, and Laxton. This "infection," or, as Darwin terms it, "the direct or immediate action of the male element on the mother form," is now generally known as *Xenia*, a term suggested by Dr Focke. Curiously enough, in all my experiments, I have never yet met with a clear case, though I have often suspected it. In some cases, however, I quite appreciate that even if it did occur it would be a difficult matter to establish it clearly. Professor Correns goes so far as to doubt it altogether (1901), but Mr Bateson regards it as a substantial fact in *certain races* (1902, p. 139). In view of all the complications it will be seen how absolutely necessary it is to regard the cotyledon colour altogether apart from the seed-coat colour.

Ordinary garden Peas have as a rule cotyledons either yellow or green.

The precise shades of these colours vary in different races, in different Peas of the same race, and even in the cotyledons of the same Pea. Generally speaking, however, I have found many races quite constant, much more so, indeed, than in seed shape.

With regard to the nature of the two colours, Mr Bateson admirably puts it: "In the green certain pigmentary matters persist in the ripe seed which disappear or are decomposed in the yellow as the seed ripens." (1902, p. 120.) Thus it may be said that all Peas are green, but that some remain green while others change into yellow as they ripen. It has been the custom, apparently, for most observers to take the cotyledon colour of a Pea from the outer surface only: that is, the surface immediately beneath the seed-coat (*cf.* Weldon, 1902, pl. I.); but in my experiments I have not found that to be a true test of cotyledon colour. I prefer to separate the cotyledons and observe the internal colour also. True yellow cotyledons have usually the outer layer yellow, while the larger area within is creamy yellow, shading to white. True green cotyledons have usually the outer layer green, though sometimes

this is yellowish or even clear yellow, but the larger area within is always green, shading to a lighter green. In the 'Eclipse' race, for instance, I have found odd seeds which, when peeled, had apparently yellow cotyledons instead of the usual green, but when the cotyledons were separated they were found to be quite green in the large area within.

In dealing with cotyledon colour it therefore seems necessary to observe the inner surface of the cotyledons as well as the outer.

The sub-races of the 'British Queen,' used as a parent in the experiments, had the outer surface of the cotyledons a deep shade of yellow, which, following Professor Weldon's colour scale (1902, pl. I., figs. 1-12), compares best with fig. 5; the inner surface of the cotyledons was creamy white. This dark yellow sub-race proved quite constant from seed. The sub-race of 'Eclipse,' used as a parent in the experiments, had the outer surface of the cotyledons a deep shade of green, which was a full shade darker than the darkest green shown on Professor Weldon's colour scale, fig. 1; the inner surface of the cotyledons was a lighter shade of green. This dark green sub-race proved quite constant from seed.

First Generation (F₁).

EXPERIMENT 1.—'British Queen' ♀ × 'Eclipse' ♂.

(Yellow ♀ × Green ♂.)

As previously described, a single plant of 'British Queen' was crossed with pollen of a single plant of 'Eclipse,' and produced 19 hybrid seeds, all of which had yellow cotyledons when dried, thus once more demonstrating the dominance of yellow cotyledons over green, and confirming the previous experiments of Mendel (1865), Correns (1900), Tschermak (1900, 1901), and Bateson (1902). Three of these hybrid yellow seeds were peeled and the cotyledons separated; two were retained whole for reference, and the remainder were sown, a slight portion of the seed-coat having been previously removed from each to compare the actual shade of the outer surface of the cotyledons with those that were peeled and separated. The outer surface of the cotyledons in all these dominant hybrids was found to be an intense shade of yellow, but curiously enough all were uniformly a darker shade of yellow than the pure dominant parent 'British Queen,' thus being a shade darker than Professor Weldon's darkest fig. 5 (1902, pl. I.).

This increased intensity of tint in the dominant hybrids of the first generation was quite unexpected; but, as the sequel shows, the results of the second generation provide a clue to the mystery. The inner surface of the cotyledons in those examined was creamy yellow, being also darker than the pure dominant, which was creamy white.

In the first generation, therefore, the dominance of yellow cotyledons over green was absolute and exclusive, there being no trace of green either without or within the cotyledons. As shortly to be seen, the green colour, though not patent in the first generation, was nevertheless latent, reappearing in full strength in the second generation, exactly as Mendel demonstrated (Mendel 1865, Bateson 1901).

Second Generation (F₂).

DR × DR.

Fourteen of the dominant yellow hybrids raised in Experiment 1 were sown, and, as previously described, produced 12 hybrid plants which, self-fertilised, gave 1755 seeds in the second generation. The cotyledons of these seeds were of two distinct colours, yellow or green, both colours being often produced in the same pod; some pods contained all yellow, but none contained all green. The following is a list of the numbers of each colour produced by the individual plants:

Expt.	D Yellow	R Green
2	23	10
3	27	9
4	26	9
5	374	129
6	11	9
7	134	37
8	57	17
9	205	50
10	284	110
11	84	31
12	71	26
13	14	8
Total	1310	445
Actual ratio ...	2.9 D	: 1 R
Mendelian ratio	3 D	: 1 R

Out of the 1755 seeds of the second generation, 1310 were yellow dominants and 445 green recessives, giving a ratio of 2.9 D : 1 R, which is close to the 3 : 1 expected by Mendel's law. With regard to the precise nature of the dominant and recessive categories in the above experiments, the character of cotyledon colour is apparently much more simple than that of seed shape, possibly being less influenced by the conditions of life.

One hundred full-sized healthy seeds of the yellow *round* Peas were taken at random from Experiments 2, 3, 4, 6, 7, 8, 11, 12, and 13 (those of Experiments 5, 9, and 10 being required for sowing), and when peeled they were all quite indistinguishable in colour from the yellow *round* hybrid Peas of the first generation, both without and within the cotyle-

dons. Similarly, 50 yellow *wrinkled* Peas from the same experiments were indistinguishable both in colour and in shape from the pure yellow *wrinkled* Peas of the 'British Queen' grand-parent. The wrinkled yellows compared well with Professor Weldon's fig. 5, while the round yellows were a full shade darker. (1902, pl. I.)

In the same way fifty of the green *round* Peas were found to be indistinguishable in colour from the pure green round 'Eclipse' grand-parent, while the green *wrinkled* Peas were a full shade lighter. The wrinkled greens compared well with Professor Weldon's fig. 1, while the round greens were a full shade darker (1902, pl. I.). It is evident therefore that the round Peas, both yellow and green, are throughout the experiment a full shade darker in colour than the corresponding wrinkled ones; and this apparently explains the fact of the dominant hybrids of the first generation being a shade darker than the pure dominant, the former being round while the latter was wrinkled. This suggests that the shade of colour depends upon other factors than heredity, and it would be interesting to know why the wrinkled Peas are a lighter colour than the round ones of similar breeding. Possibly the premature conversion of starch in the wrinkled Peas (if it occurs) may have some effect on the intensity of colour.

In the above experiments the yellow and green colours are perfectly discontinuous, with no trace of the intermediate shades of 'Telephone' and 'Stratagem' shown in Professor Weldon's colour scale (1902, pl. I.).

COMBINATION OF TWO CHARACTERS.

Seed Shape and Cotyledon Colour.

Hitherto we have dealt with seed shape and cotyledon colour in Peas as single characters, but the practical advantages of the Mendelian principles become even more pronounced when we deal with two or more characters in combination in individual plants or races.

In the first generation the Wrinkled yellow 'British Queen' was crossed with the Round green 'Eclipse,' and all the 19 hybrids were of one type, Round yellow.

In the second generation the Mendelian expectation is 4 distinct types, viz. round yellow, round green, wrinkled yellow, and wrinkled green, in the respective ratios of 9 : 3 : 3 : 1. All the possible combinations are effected, the frequency being according to the calculus of chance based on the Mendelian ratios of 3 round to 1 wrinkled and 3 yellow to 1 green. Below is a list of the actual numbers of each of the 4 types produced by the individual plants in Experiments 2-13.

From the following table it will be observed that each of the expected types occurs in the second generation in accordance with Mendel's law, and that the numbers observed of each type are close to the numbers calculated by means of the Mendelian ratios. The production of these four types in the second generation proves that seed shape and cotyledon colour are two distinct characters, each with a separate and independent inheritance, and that each character must therefore be represented in the germ-cells or gametes by a distinct unit. The appreciation of this elementary fact enabled Mendel to make his discoveries in heredity. All the statistical experiments in the heredity of animals and plants now being carried on by many experimenters in Europe and America are based upon this simple Mendelian idea of unit-characters (also discovered independently by Professor De Vries before he re-discovered Mendel's long-lost paper, 1900 A, B). Naturally Mendel himself was only able to touch the fringe of the subject in his experiments with Peas; yet, by making this one point clear, he has enabled his many successors to attack the difficult and complicated problem in a new and analytical way. Already, by the application of the Mendelian system of analysis by experiment, there are signs that we are on the eve of some important discoveries in heredity.

	Expt.	Round Yellow	Round Green	Wrinkled Yellow	Wrinkled Green
	2	19	8	4	2
	3	24	8	3	1
	4	17	7	9	2
	15	281	97	93	32
	6	8	7	3	2
	7	109	26	25	11
	8	49	13	8	4
	9	161	42	44	8
	10	203	84	81	26
	11	62	23	22	8
	12	54	18	17	8
	13	10	5	4	3
Observed	...	997	338	313	107
Calculated	...	990	330	330	110
Mendelian ratio...	...	9	: 3	: 3	: 1

¹ In 1905 the round yellow seeds of one of the F_3 plants of this experiment were sent to the late Mr A. D. Darbishire who continued the experiments up to the time of his lamented death in 1915. The experiments were carried on by Miss Darbishire and Mr Frank Sherlock to the F_{17} generation in 1918 and the data of generations F_{12} — F_{17} have been statistically reduced and reported on by Mr G. Udny Yule, F.R.S., in *Journal of Genetics*, 1923, XIII. pp. 255—331. (Note added 1925.)

(Since the above was written, I find that Mr R. P. Gregory, in a recent paper on "The Seed Characters of *Pisum sativum*" (*New Phytologist*, 1903, December, p. 226, fig. 1), shows clearly that the histological nature of a "Round" Pea is quite distinct from that of a "Wrinkled" one. In a "Round" Pea the starch grains, stored in the cotyledons, are large, few, and oval, while in a "Wrinkled" Pea they are small, numerous, and irregular.

In examining some of the "intermediate" and dubious shapes pointed out by Professor Weldon in such irregular round races as 'Telegraph' (1902, pl. II. figs. 1-4), Mr Gregory found no seed which, upon histological examination, allowed of any doubt as to its round character.

Mr Gregory concludes therefore that pitting, false wrinkling, and other irregularities in "Round" Peas must be distinguished from the true wrinkling in "Wrinkled" Peas, and that the latter must be the expression of a distinct physiological process. These important histological observations show the necessity of caution in ascribing irregularities of seed shape in Peas to a failure of Mendelian dominance or segregation; and, as my own experiments show, there is little doubt that some at all events of these irregularities are due to the various influences of the conditions of life, rather than to heredity.)

REFERENCES.

- BATESON, W. (1901). English translation of Mendel's original paper, with introduction. *Journ. Roy. Hort. Soc.* xxvi. p. 1.
- (1902). Mendel's Principles of Heredity (with portrait of Mendel, bibliography and translations of Mendel's papers), xiv + 212 pp. (Cambridge University Press.)
- CORRENS, C. (1900). G. Mendel's Regel über das Verhalten des Nachkommenschaft der Rassenbastarde. *Ber. deut. bot. Ges.* xviii. p. 158.
- (1901). Bastarde zwischen Maisrassen, mit besonderer Berücksichtigung der Xenien. *Bibliotheca Botanica*, Heft 53.
- DARWIN, C. (1868). The Variation of Animals and Plants under Domestication. Second edition, 1893, Vol. I.
- DE VRIES, H. (1900). (a) Sur la Loi de Disjonction des Hybrides. *Comptes Rendus*, March 26, 1900.
- (1900). (b) Das Spaltungsgesetz der Bastarde. *Ber. deut. bot. Ges.* 1900, xviii. p. 83. (English translation in *Journ. Roy. Hort. Soc.* 1901, xxv. p. 243.)
- KNIGHT, T. A. (1799). An Account of some Experiments on the Fecundation of Vegetables. *Phil. Trans.* Pt. II. p. 195.
- MENDEL, G. (1865). Versuche über Pflanzen-Hybriden. *Verh. naturf. Ver. in Brünn*, Band IV., *Abhandlungen*, p. 1. (English translation in *Journ. Roy. Hort. Soc.* 1901, xxvi. p. 1.)
- SHERWOOD, N. N. (1899). Garden Peas. *Journ. Roy. Hort. Soc.* xxii. p. 239.
- TSCHERMAK, E. (1900). Ueber künstliche Kreuzung bei *Pisum sativum*. *Ztschrift. f. d. landwirts. Versuchswesen in Oesterr.* III. p. 465.
- (1901). *Ibid.* IV. p. 641, and p. 1029.
- WELDON, W. F. R. (1902). Mendel's Laws of Alternative Inheritance in Peas. *Biometrika*, I. Pt. II. (Jan.) p. 228, plates I. and II.

XI

EXPERIMENTS ON HEREDITY IN RABBITS¹

An inbred pair of albino Angoras was crossed reciprocally with an inbred pair of Belgian hares (F_1), and the hybrid progeny were bred with one another for two generations (F_2 and F_3). Four characters were under observation, each of which was inherited independently of the other.

1. *Angora Coat*.—In F_1 the Angora coat was always recessive to the normal coat, which was completely dominant. In F_2 and F_3 this pair of structural characters followed the Mendelian laws of segregation and gametic purity simply and without exception.

2. *Albinism*.—In F_1 the albino character was always recessive to the normal character, which was dominant, and in F_2 and F_3 followed the ordinary Mendelian rules.

3. *Coat Colour*.—In F_1 brown-grey \times albino gave all with wild grey coats. In F_2 the hybrid greys bred together gave a ratio of

9 grey : 3 black : 4 albino.

Experiments in F_3 proved that the black factor was not introduced by the original brown parent, but *by the albino*, which, though gametically pure as regards simple albinism, was at the same time carrying the distinct factor for black coat-colour.

These results in rabbits confirm the important results already gained by Cuénot in mice.

The F_2 greys proved to be of four kinds—viz., pure grey, grey containing black, grey containing albino, and grey containing black and albino. The F_2 blacks were of two kinds—viz., pure black and black containing albino. The F_2 albinos were of three kinds—viz., albino containing grey, albino containing black, and albino containing grey and black. These results are in accordance with the Mendelian expectation, which is—

$$\underbrace{1G : 2G(B) : 2G(A) : 4G(B)(A)}_{9 \text{ grey}} : \underbrace{1B : 2B(A)}_{3 \text{ black}} : \underbrace{1A(G) : 2A(G)(B) : 1A(B)}_{4 \text{ albino}}$$

¹ Read before Section "D" at the Cambridge Meeting of the British Association for the Advancement of Science, 19th Aug. 1904, and reprinted from *Report Brit. Assoc. Cambridge*, 1904, pp. 592–593 (1905).

One point, however, remains to be cleared up, and that is, the absence of brown-greys in F_2 and F_3 , these being in all cases apparently displaced by greys.

4. *Dutch Markings*.—In F_1 the offspring from one albino were, as a rule, uniform in colour, like the coloured parent, while those from the other albino were all more or less marked with white on the fore extremities. In F_2 and F_3 the uniform hybrids were, as a rule, constant, while the marked ones produced a proportion of true Dutch-marked rabbits, as well as the ordinary-marked and some uniform ones.

These results suggest that one albino contained the factor for Dutch markings while the other albino did not. Experiments are now in progress to work out this interesting question.

XII

EXPERIMENTAL STUDIES ON HEREDITY IN RABBITS¹

The following experiments were designed in 1902 with the object of determining whether the Mendelian principles of heredity were applicable to animals as well as plants. For that purpose the domestic Rabbit seemed to be a likely subject, as many of the fancy races were well known to possess distinct structural and colour characters which constantly bred true.

At first, in order to make the experiments as simple as possible, two races only were selected for crossing, White Angora and Belgian Hare (fig. 93). The former is an albino race with pink eyes, swaying habit, and a long Angora coat of fine texture; while the latter is a normal race with pigmented skin, dark eyes, and short yellow-grey fur of coarser texture. An inbred pair of each race was crossed reciprocally, and the hybrids of the first generation were all normal individuals with pigmented skin, dark eyes, short fur, and grey coat like that of the common wild rabbit. Those by the albino buck were all self-coloured, while those from the albino doe were, with one exception, more or less marked with white on the fore extremities (fig. 93). These grey hybrids bred together produced 14 distinct types in the second generation, viz. (fig. 94):—

- Short, normal², grey, self-coloured.
- Short, normal, grey, marked.
- Short, normal, grey, Dutch-marked.
- Short, normal, black, self-coloured.
- Short, normal, black, marked.
- Short, normal, black, Dutch-marked.
- Short, albino³, white.

¹ Read before the Linnean Society of London, 15th Dec. 1904. Extracted from the Linnean Society's Journal—*Zoology*, xxix. pp. 283-324 (1905).

² Pigmented, with normal demeanour (see p. 174).

³ Unpigmented, with swaying habit (see p. 174).



Angora in fig. 93.

Angora, normal, grey, self-coloured.
Angora, normal, grey, marked.
Angora, normal, grey, Dutch-marked.
Angora, normal, black, self-coloured.
Angora, normal, black, marked.
Angora, normal, black, Dutch-marked.
Angora, albino, white.

All the normals had dark eyes and the albinos pink eyes. Several types appeared in the same litter, and each individual hybrid produced all the types.

This epidemic of variation in the second generation of hybrids has been the common experience of experimenters both in animals and plants, and before the Mendelian principles became known remained practically unexplained. By the aid of the Mendelian principles we are able to see at once that there are at least 4 pairs of distinct characters concerned in the offspring of the second generation, each pair being inherited independently of the others, viz.:—Short and Angora coat, normality and albinism, grey and black coat, self-coloured and marked coat.

In order to simplify such a complicated problem, each of these 4 pairs of characters will be dealt with singly, and the offspring of each individual detailed separately. To facilitate this, each individual was numbered as soon as it was used at the stud, which number is reserved solely for that individual throughout its life.

The 4 individuals used at the outset were as follows:—No. 1 doe and No. 4 buck were pure bred Belgian Hares raised out of the same litter. No. 2 buck and No. 3 doe were pure-bred White Angoras, both by the same buck but out of different does.

These 4 individuals were obtained from local fanciers, whose pure and constant strains had been under observation for several years, so that no extensive tests of their purity and constancy were deemed necessary. For the purpose, however, of securing young stock for further experiments, 4 litters, containing 28 individuals, were raised from the pair of Belgians and the pair of Angoras; all of these bred true to their parents in all the characters with which we are concerned.

(1) SHORT AND ANGORA COAT.

The coat of the "Belgian Hare" rabbit, in common with that of the wild rabbit and most of the domesticated races, is made up of short coarse fur, the longest hairs of which seldom exceed 2.5 cm.

The coat of the Angora race consists of long, fine wool, the longest hairs of which often exceed 15 cm.

The two kinds of coat are unmistakable, not only in the extreme difference in their length, but also in their texture. The Angora coat is finer and softer in texture than the short coat, and, unless constantly combed out, quickly becomes matted and woolly, unlike the short fur, which lies back quite flat.

As already noted, both kinds of coat breed true when mated with their own kind.

(a) First Generation (F₁).

No. 1 doe with short coat mated with No. 2 buck with Angora coat produced 26 hybrids with short coats.

The reverse cross, No. 3 doe with Angora coat mated with No. 4 buck with short coat, produced 16 hybrids with short coats. In general appearance the hybrid short coats were indistinguishable from the pure short coat, the influence of the Angora character not being apparent. A careful examination, however, revealed what appeared to be faint traces of the Angora influence in both length and texture. The hairs of the hybrid coat were slightly longer, seemed softer to the touch, and were apparently more densely distributed than in the pure short coat. At the same time it must be admitted that these apparent traces of the Angora influence were so small, that had one not known the Angora parentage it would never have been suspected. In Mendelian terms, therefore, short coat may be said to be dominant over Angora coat, which is recessive.

Further experiments recently carried out show that the short coat of other races, as well as the Belgian Hare, is similarly dominant over the Angora coat. Altogether, 87 hybrids have been raised by crossing shorts with Angoras, and all have short coats, no matter whether the Angora was used as the male or female parent. It appears, therefore, that in these cases the phenomenon of dominance is peculiar to the character itself, and is not in any way influenced by change of sex, change of individual, or change of race.

The following table gives the results of the individual matings. S = pure short coat, A = pure Angora coat, and the numbers attached to these letters refer to the individual animals used. To save repetition, it may be noted that the doe is placed first throughout the matings; *e.g.* S 1 \times A 2 is No. 1 doe with short coat mated with No. 2 buck with Angora coat; Nos. 1, 4, 13, and 25 are Belgian Hares, No. 47 is a Silver Fawn, Nos. 51 and 52 are Dutch, No. 61 is a Himalayan, and Nos. 2, 3, 23, and 50 are Angoras.

TABLE 1.
Shorts \times Angoras (F_1).

Matings	Short	Angora
S 1 \times A 2 	26	0
A 3 \times S 4 	16	0
A 3 \times S 51 	8	0
S 13 \times A 2 	4	0
A 23 \times S 25 	13	0
A 23 \times S 61 	7	0
A 50 \times S 47 	8	0
S 52 \times A 2 	5	0
Total 	87	0

(b) Second Generation (F_2).

The short-coated hybrids of the first generation bred together produced a mixture of shorts and Angoras in Mendelian proportions. 7 short-coated hybrids bred together produced 171 young, of which 70 were reared to the age of two months or more, when the nature of the coat became evident; of these, 53 had short coats and 17 were Angoras.

The Mendelian expectation for 68 young is 51 shorts and 17 Angoras.

The Angora coats of the second generation were indistinguishable from those of pure-bred Angoras of the same age.

The short coats of the second generation were similar in appearance to those of the pure and hybrid shorts.

Each individual hybrid of the first generation that was tested produced both kinds of coat, usually in the same litter.

The individual results were as follows:—No. 5 gave 6 shorts and 3 Angoras; No. 7, 8 S and 3 A; No. 8, 2 S and 2 A; No. 9, 24 S and 5 A; No. 10, 37 S and 11 A; No. 11, 13 S and 4 A; No. 12, 16 S and 6 A.

The following table gives the individual matings with the details of each litter. H = hybrid of the first generation bred from S \times A.

TABLE 2.

Hybrid Shorts bred together (F ₂).					
Matings				Short	Angora
H 5 \times H 12	5	2
H 5 \times H 10	1	1
H 7 \times H 10	2	1
H 7 \times H 10	2	1
H 7 \times H 10	4	1
H 8 \times H 10	1	1
H 8 \times H 10	1	1
H 9 \times H 10	7	1
H 9 \times H 10	5	2
H 9 \times H 10	2	1
H 9 \times H 10	4	0
H 9 \times H 10	6	1
H 11 \times H 12	5	2
H 11 \times H 12	6	2
H 11 \times H 10	2	0
Total	53	17

The short-coated hybrids of the first generation mated back with the original Angoras produced a mixture of shorts and Angoras in Mendelian proportions. 5 short-coated hybrids mated with Angoras produced 54 young, of which 38 were reared; of these, 20 had short coats similar in appearance to those of the pure and hybrid shorts, while 18 were Angoras indistinguishable from the pure Angoras. The Mendelian expectation for this mating is 19 shorts and 19 Angoras.

Curiously enough, in the first litter H 8 \times A 2 produced 5 young, *all Angoras*, while in the second litter there were 3 shorts and 3 Angoras, as expected. The following table gives the numbers obtained in each litter from the individual matings:—

TABLE 3.

Hybrid Shorts \times Angoras (F).					
Matings				Short	Angora
H 5 \times A 2	3	2
H 5 \times A 2	5	2
H 7 \times A 2	4	3
H 8 \times A 2	0	5
H 8 \times A 2	3	3
A 3 \times H 10	3	3
A 3 \times H 12	2	0
Total	20	18

2 short-coated hybrids of the first generation mated back with the original short produced 20 young, of which 17 were reared. All had short coats similar in appearance to the pure and hybrid shorts, in accordance with the Mendelian expectation.

The matings were as follows:—S1 × H12 gave 11 shorts in two litters, and S1 × H10 gave 6 shorts in one litter.

(c) *Third Generation (F₃).*

The Angoras of the second generation extracted from the hybrid shorts of the first generation bred quite true when mated together and with pure-bred Angoras.

9 extracted Angoras mated together and with Angoras produced 41 Angora young, all indistinguishable from pure-bred Angoras, in accordance with the Mendelian expectation. 26 of these were raised from the extracted Angoras bred together.

The individual matings were as follows. EA = Extracted Angora. Nos. 26, 33, 37, 53, and 54 were extracted from H × H, while Nos. 16, 20, 41, and 42 were extracted from H × A.

TABLE 4.

Extracted Angoras × Angoras (F ₃).					
Matings				Short	Angora
EA 16 × A 2	0	5
EA 20 × A 2	0	4
EA 33 × A 24	0	6
EA 33 × EA 37	0	7
EA 42 × EA 26	0	6
EA 53 × EA 37	0	7
EA 54 × EA 41	0	6
Total	0	41

The extracted Angoras, like the pure-bred Angoras, proved to be recessive to pure shorts. 4 extracted Angoras mated with 3 pure and 1 extracted short produced 27 short-coated young, similar in appearance to the pure and hybrid shorts.

The matings were as follows (ES = Extracted pure Short):—

TABLE 5.

Extracted Angoras × Pure Shorts (F ₃).					
Matings				Short	Angora
EA 15 × S 25	6	0
EA 15 × S 51	8	0
EA 16 × S 61	7	0
ES 34 × EA 37	6	0
Total	27	0

The extracted Angoras, like the pure-bred Angoras, gave a mixture of shorts and Angoras when mated with hybrid shorts. 5 extracted Angoras mated with 3 hybrid shorts produced 28 young, of which 17 had short coats and 11 Angoras. The Mendelian expectation is 14 shorts and 14 Angoras.

It will be observed that there is here a slight excess of shorts, which appears to be due to EH 28 giving 12 shorts and 6 Angoras instead of the expected 9 of each. The matings were as follows:—

TABLE 6.

Extracted Angoras × Hybrid Shorts (F ₃).					Short	Angora
Matings						
EA 15 × H 12	2	2
EA 15 × EH 28	3	1
EA 16 × EH 28	4	2
EA 16 × EH 28	1	0
EA 20 × EH 28	2	2
EA 33 × EH 28	2	1
EH 31 × EA 26	3	3
Total	17	11

From the above experiments with 10 Angoras extracted from hybrid shorts, it is clear that the extracted Angoras are not only indistinguishable in appearance from pure-bred Angoras, but in their breeding they behave exactly as do the pure-bred Angoras, viz.:—(1) They breed true with one another; (2) they are recessive to pure shorts; (3) they give mixed offspring when mated with hybrid shorts.

These facts are all in accordance with the Mendelian conception of gametic purity, and there seems to be no doubt that, notwithstanding their hybrid origin, these extracted Angoras are pure Angoras, giving off gametes carrying the Angora factor simply, with no trace of the short-coat factor carried (in the case of 5 of them) by both their parents and one-half of their ancestors for several generations and probably many more.

The short-coated individuals of the second generation tested with Angoras and hybrids proved to be of two kinds, pure shorts and hybrid shorts, the former producing all shorts and the latter a mixture of shorts and Angoras.

Out of 16 individuals tested, 5 were extracted from hybrids of the first generation mated back with the original Angoras (H × A), and these all proved to be hybrids in accordance with the Mendelian expectation.

One individual was extracted from a hybrid of the first generation mated back with one of the original shorts ($H \times S$), and this proved to be a hybrid, the Mendelian expectation for 2 such individuals being 1 pure and 1 hybrid.

The remaining 10 individuals were extracted from hybrids of the first generation bred together ($H \times H$), and of these 4 proved to be pure and 6 were hybrids; the Mendelian expectation for 12 such individuals being 4 pure and 8 hybrids.

The 4 pure extracted shorts mated with 3 Angoras and 4 hybrids produced 51 short-coated young, similar in appearance to the pure and hybrid shorts. The matings were as follows:—

TABLE 7.

Extracted Shorts \times Angoras and Hybrids (F_3).

Matings	Short	Angora
ES 30 \times H 10	5	0
ES 30 \times H 10	7	0
ES 32 \times A 2	5	0
ES 32 \times H 12	4	0
ES 32 \times H 10	5	0
ES 34 \times EA 37	6	0
ES 34 \times EH 14	5	0
ES 36 \times EH 28	3	0
ES 36 \times H 10	5	0
ES 36 \times EA 26	6	0
Total	51	0

The extracted hybrid shorts mated together and also with Angoras in each case produced a mixture of shorts and Angoras in Mendelian proportions. 10 extracted hybrids mated together and with 2 hybrids of the first generation produced 41 young, of which 31 had short coats and 10 were Angoras; the Mendelian expectation for 40 young is 30 shorts and 10 Angoras. The matings were as follows:—

TABLE 8.

Extracted Hybrids \times Hybrids (F_3).

Matings	Short	Angora
EH 18 \times EH 14	2	3
EH 21 \times EH 14	5	2
EH 21 \times EH 38	5	2
EH 29 \times H 10	3	0
EH 29 \times EH 27	3	1
EH 31 \times H 12	4	0
EH 35 \times EH 28	3	1
EH 35 \times EH 28	2	0
EH 45 \times EH 28	4	1
Total	31	10

7 extracted hybrids mated with 8 Angoras produced 50 young, of which 27 had short coats and 23 were Angoras; the Mendelian expectation is 25 shorts and 25 Angoras. The matings were as follows:—

TABLE 9.

Extracted Hybrids \times Angoras (F_3).

Matings				Short	Angora
EH 17 \times A 2	2	3
EH 18 \times A 2	2	1
EH 19 \times A 2	1	1
EH 21 \times A 2	2	2
A 23 \times EH 28	2	2
EA 15 \times EH 28	3	1
EA 16 \times EH 28	1	1
EA 16 \times EH 28	4	2
EA 20 \times EH 28	2	2
EH 31 \times EA 26	3	3
EA 33 \times EH 28	2	1
EH 44 \times A 24	3	4
Total	27	23

From the above results it would appear that the unit characters, short and Angora coat, in their heredity follow the Mendelian type *Pisum* as regards dominance, segregation, and gametic purity.

(2) NORMALITY AND ALBINISM.

The normal Belgian rabbit has a pigmented skin, coloured coat, dark eyes, and normal demeanour, while the albino Angora has a clear skin devoid of pigment, white coat, pink eyes, and a curious habit of swaying the head from side to side whenever the body is at rest. So far as these experiments go, all these apparently different characters of the albino are correlated and inherited as a single character or unit, which may be simply called albinism as opposed to normality.

In describing these experiments, therefore, it will be understood that the term normal includes a pigmented skin, coloured coat, dark eyes, and normal demeanour, while the term albino comprises a clear skin, white coat, pink eyes, and the swaying habit. As already noted, both the normal Belgians and the albino Angoras breed true when mated with their own kind.

(a) First Generation (F_1).

No. 1 normal doe mated with No. 2 albino buck produced 26 normal hybrids. The reverse cross, No. 3 albino doe mated with No. 4 normal buck, produced 16 normal hybrids. The 26 normal hybrids of the first cross did not show the slightest trace of the albino parentage in any respect. The 16 normal hybrids of the reverse cross (with one exception) had a few white markings on the fore extremities, but, as will be seen later, these do not seem to be connected with simple albinism at all, but rather with the Dutch markings latent in the albino (see under Sect. 4, p. 192). In Mendelian terms, therefore, normality may be said to be dominant over albinism, which is recessive.

Further experiments recently carried out show that the normal character of other races as well as the Belgian is similarly dominant over albinism. Altogether 94 hybrids have been raised by crossing normal and albino individuals and all have proved to be normal hybrids, whether the albino was used as the male or the female parent. It appears that in these cases also the phenomenon of dominance is peculiar to the character itself, and is not influenced by change of sex, individuals, or race. The individual matings were as follows. N = normal, A = Albino. No. 47 is a Silver Fawn; Nos. 51 and 52 are Dutch; Nos. 1, 4, 13, and 25 are Belgians; and Nos. 2, 3, 6, 23 and 50 are Angoras.

TABLE 10.

Matings	Normal \times Albino (F_1).			Normal	Albino
		
N 1 \times A 2	26	0
A 3 \times N 4	16	0
A 3 \times N 51	11	0
A 6 \times N 4	8	0
N 13 \times A 2	4	0
A 23 \times N 25	16	0
A 50 \times N 47	8	0
N 52 \times A 2	5	0
Total	94	0

(b) Second Generation (F_2).

The normal hybrids of the first generation bred together produced a mixture of normals and albinos in Mendelian proportions. 7 normal hybrids bred together produced 171 young, of which 132 were normal and 39 were albinos. The Mendelian expectation for 172 young is 129 normals and 43 albinos.

Each individual hybrid that was tested produced both normals and

albinos, usually in the same litter. The individual results were as follows:—No. 5 gave 13 normals and 4 albinos; No. 7, 22 N and 9 A; No. 8, 28 N and 4 A; No. 9, 43 N and 14 A; No. 10, 92 N and 24 A; No. 11, 26 N and 8 A; and No. 12, 40 N and 15 A.

It will be observed that No. 8 gives a decided *deficiency* of albinos, while, as will be seen later, the same individual in a previous litter gave an unexpected *excess* of albinos when mated with an albino.

The albinos of the second generation extracted from the normal hybrids of the first generation had apparently the same albinic characters as the original albino grand-parents, viz. a clear skin devoid of pigment, pure white coat, pink eyes, and the swaying habit.

The normals of the second generation had apparently the same normal characters as the original normal grand-parents and the normal parents, viz. a pigmented skin, coloured coat, dark eyes, and normal demeanour. The majority were self-coloured like the original normals, while some were slightly marked with white on the fore extremities, and a few were marked like the pure Dutch rabbit. As will be seen later, these Dutch markings are apparently not connected with simple albinism (see under Sect. 4, p. 192).

The following table gives the individual matings with the details of each litter:—

TABLE 11.
Hybrid Normals bred together (F₂).

Matings				Normal	Albino
H 5 × H 12	6	3
H 5 × H 10	7	1
H 7 × H 10	4	4
H 7 × H 10	3	1
H 7 × H 10	7	2
H 7 × H 12	8	2
H 8 × H 10	8	1
H 8 × H 10	8	1
H 8 × H 10	8	1
H 8 × H 10	4	1
H 9 × H 10	8	0
H 9 × H 10	5	2
H 9 × H 10	6	2
H 9 × H 10	7	1
H 9 × H 10	7	2
H 9 × H 10	4	3
H 9 × H 12	6	4
H 11 × H 12	6	2
H 11 × H 12	7	1
H 11 × H 12	7	3
H 11 × H 10	6	2
Total	132	39

The normal hybrids of the first generation bred back with the original albinos produced a mixture of normals and albinos in Mendelian proportions.

5 normal hybrids mated with 2 albinos produced 54 young, of which 25 were normals and 29 were albinos. The Mendelian expectation is 27 normals and 27 albinos. Each hybrid tested produced both kinds, usually in the same litter, but, curiously enough, H 8 \times A 2 gave in the first litter 5 young *all albinos*, while in the second litter there were 6 normals and 2 albinos, instead of the expected 4 of each. It will be noted that H 8 was the individual which gave a *deficiency* of albinos in the 4 succeeding litters when mated with H 10. The individual matings were as follows:—

TABLE 12.

Hybrid Normals \times Albinos (F_2).					
Matings				Normal	Albino
H 5 \times A 2	2	2
H 5 \times A 2	4	1
H 5 \times A 2	3	4
H 7 \times A 2	3	4
H 8 \times A 2	0	5
H 8 \times A 2	6	2
A 3 \times H 10	4	2
A 3 \times H 10	2	5
A 3 \times H 12	1	4
Total	25	29

2 normal hybrids of the first generation mated with one of the original normals produced 20 young, all normals. The matings were N 1 \times H 12, producing 11 young in 2 litters, and N 1 \times H 10, producing 9 young in 1 litter. The Mendelian expectation is, of course, all normals.

(c) *Third Generation (F_3).*

The albinos of the second generation extracted from the hybrid normals of the first generation bred true when mated with one another and with other albinos, in accordance with the Mendelian expectation.

4 extracted albinos mated together and with 2 other albinos produced 21 young, all of which were albinos. The matings were as follows:—

TABLE 13.

Extracted Albinos \times Albinos (F_3).

Matings	Normal	Albino
EA 16 \times A 2	0	5
EA 16 \times A 61	0	7
EA 34 \times EA 14	0	5
EA 45 \times A 61	0	4
Total	0	21

The extracted albinos, like the pure-bred albinos, proved to be recessive to pure normals.

6 extracted albinos mated with 3 pure and 3 extracted normals produced 62 young, all of which were normals, in accordance with the Mendelian expectation.

The individual matings were as follows (EN = Extracted pure normal):—

TABLE 14.

Extracted Albinos \times Pure Normals (F_3).

Matings	Normal	Albino
EA 15 \times N 25	6	0
EA 15 \times EN 28	4	0
EA 15 \times N 51	8	0
EA 16 \times EN 28	6	0
EA 16 \times EN 28	6	0
EA 34 \times N 49	8	0
EA 39 \times N 51	2	0
EA 39 \times N 51	6	0
EN 43 \times EA 14	7	0
EN 44 \times EA 14	4	0
EA 45 \times EN 28	5	0
Total	62	0

The extracted albinos, like the pure-bred albinos, gave a mixture of normals and albinos in Mendelian proportions when mated with hybrid normals. 5 extracted albinos mated with 6 hybrid normals produced 47 young, of which 23 were normals and 24 were albinos. The Mendelian expectation for 48 young is 24 normals and 24 albinos.

The matings were as follows (EH = Extracted hybrid):—

TABLE 15.

Extracted Albinos \times Hybrid Normals (F_3).					
Matings			Normal	Albino	
EA 15 \times H 12	4	3	
EH 18 \times EA 14	4	2	
EH 19 \times EA 14	1	4	
EH 19 \times EA 14	2	4	
EH 21 \times EA 38	5	2	
EH 21 \times EA 14	3	4	
EA 34 \times EH 37	2	4	
EA 39 \times EH 41	2	1	
Total	23	24	

From the above experiments with albinos of the second generation extracted from the normal hybrids of the first generation it is clear that not only are the extracted albinos indistinguishable in their albinism from the pure-bred albinos, but in their breeding they behave precisely as do the pure-bred albinos, viz.:—(1) They breed true with one another; (2) they are recessive to pure normals; (3) they give mixed offspring when mated with hybrid normals. These facts are all in accordance with the Mendelian conception of gametic purity; and there seems to be no doubt that, notwithstanding their hybrid origin, these extracted albinos are pure albinos.

The normal individuals of the second generation, tested with albinos and hybrids, proved to be of two kinds, pure and hybrid; the former producing all normals, and the latter a mixture of normals and albinos. Out of 21 individuals tested, 7 were extracted from hybrids of the first generation mated back with the original albinos ($H \times A$), and these all proved to be hybrids in accordance with the Mendelian expectation. 2 individuals were extracted from 2 hybrids of the first generation mated back with the original normal ($H \times N$), and these have so far proved to be pure normals; the Mendelian expectation for 2 such individuals is 1 pure and 1 hybrid. The remaining 13 individuals were extracted from hybrids of the first generation bred together ($H \times H$), and of these 4 proved to be pure normals and 9 were hybrid normals; the Mendelian expectation for 12 such individuals is 4 pure and 8 hybrids.

The 6 pure extracted normals mated with 4 albinos and 8 hybrids

produced 83 young, all normals in accordance with the Mendelian expectation. The individual matings were as follows:—

TABLE 16.

Extracted Normals \times Albinos and Hybrids (F_3).

Matings	Normal	Albino
H 7 \times EN 28	7	0
A 23 \times EN 28	6	0
EN 32 \times A 2	7	0
EN 44 \times A 24	7	0
EH 20 \times EN 28	6	0
EN 30 \times H 10	5	0
EN 30 \times H 10	7	0
EN 32 \times H 12	5	0
EN 32 \times H 10	5	0
EN 32 \times H 10	6	0
EH 33 \times EN 28	6	0
EN 35 \times EH 26	6	0
EH 36 \times EN 28	3	0
EN 43 \times EA 14	7	0
Total	83	0

The extracted hybrid normals mated together, and also with albinos, in each case produced a mixture of normals and albinos in Mendelian proportions. 10 extracted hybrids mated together and with 2 hybrids of the first generation produced 55 young, of which 38 were normals and 17 were albinos; the Mendelian expectation for 56 young is 42 normals and 14 albinos. The excess of albinos appears to be due to the peculiarity of EH 26, which gave 11 normals and 9 albinos instead of the expected 15 and 5. The individual matings were as follows:—

TABLE 17.

Extracted Hybrids \times Hybrids (F_3).

Matings	Normal	Albino
EH 29 \times H 10	5	2
EH 29 \times EH 27	5	1
EH 31 \times H 12	3	1
EH 31 \times EH 26	3	3
EH 36 \times H 10	4	1
EH 36 \times EH 26	4	4
EH 42 \times EH 26	4	2
EH 53 \times EH 37	6	1
EH 54 \times EH 41	4	2
Total	38	17

8 extracted hybrids mated with 5 albinos produced 89 young, of which 44 were normals and 45 were albinos; the Mendelian expectation for 90 young is 45 normals and 45 albinos. The individual matings were as follows:—

TABLE 18.

Extracted Hybrids \times Albinos (F_3).

Matings	Normal	Albino
EH 17 \times A 2	2	1
EH 17 \times A 2	5	3
EH 18 \times A 2	2	3
EH 18 \times A 2	2	3
EH 18 \times A 2	1	3
EH 18 \times EA 14	4	2
EH 18 \times A 2	4	1
EH 19 \times A 2	2	3
EH 19 \times EA 14	1	4
EH 19 \times EA 14	2	4
EH 20 \times A 2	3	1
EH 21 \times A 2	4	0
EH 21 \times A 2	2	3
EH 21 \times EA 14	3	4
EH 33 \times A 24	3	5
EA 34 \times EH 37	2	4
EA 39 \times EH 41	2	1
Total	44	45

From the above results it would appear that the unit characters normality and albinism in their heredity also follow the Mendelian type *Pisum* as regards dominance, segregation, and gametic purity.

(3) COAT COLOUR.

The grey coat of the common wild rabbit is made up for the most part of yellow hairs based and tipped with black. The extent of the coloured portions is somewhat variable in individual hairs; generally, however, the black basal portion is more extensive than the yellow middle portion, while the black apical tip is less. In these parti-coloured hairs both the yellow and black pigments occur in different dilutions. Thus, in the patch of short fluffy hairs behind the ears the yellow portion of each hair is a bright tan-yellow; while along the back, towards the tail and down the flanks on each side, the yellow becomes more diluted, passing from tan through fawn, buff, and cream to white under the tail and belly, where the yellow pigment is not

evident. In the same way the black portions of the hairs, both basal and apical, become diluted, passing from dense black through blue-black, slate-grey, and grey-white to white.

This dilution of the black pigment is especially noteworthy in the roots of the hairs, giving the impression of a blue-black ground-colour close to the skin, when the hairs are blown aside. A certain amount of chocolate or brown pigment appears to be always associated with the black.

Amongst the parti-coloured yellow and black hairs which go to form the grey coat there are a few long black hairs scattered more or less regularly, especially along the back and loins and on the ears and forehead. These long black hairs give a wavy appearance to the coat, known to fanciers as "ticking"; they are more or less shaded with brown, have blue-black roots, and do not usually appear until about the age of two months.

The above observations show that the hairs which make up the grey coat of the wild rabbit contain at least two distinct pigments—yellow and black, with their dilutions; and most probably a third, brown or chocolate, which is more or less evident in close association with the black pigment. (Cf. Mr Bateson's, Miss Durham's, and Dr Allen's observations on similar pigments in Mice: Bateson, 1903; Allen, 1904.)

The yellow-grey coat of the Belgian rabbit used in these experiments contains the same pigments, and is in all respects similar in nature to that of the wild grey, except that it contains a larger proportion of yellow pigment and less black in the individual parti-coloured hairs in all parts of the coat. This increase of yellow and reduction of black appears to affect the basal part of the hairs more than the tips.

Further, the bright tan-yellow, which is usually confined to the space behind the ears in the wild grey, is extended to the chest and flanks in the yellow-grey, though this also shades off, downward and backward, through fawn, buff, and cream, to white, as in the wild grey. The creamy-white hairs borne underneath in the wild grey have blue-black roots, giving them a grey-white appearance; while those of the yellow-grey in the same place have apparently no trace of the diluted black pigment, being almost pure white. The long black hairs also appear to be less in number in the yellow-grey than in the wild grey, and do not extend so far down the flanks. In all respects, therefore the yellow-grey has more yellow and less black pigment than the wild grey.

The yellow-grey type breeds perfectly true to the above colour-details, and can always be distinguished from the wild grey.

The coat of the albino Angora is of course pure white, with no trace of any kind of pigment.

(a) *First Generation (F₁).*

The yellow-grey Belgians crossed with the white Angoras gave hybrids all of which had wild grey coats, no matter which way the cross was made.

No. 1 yellow-grey doe mated with No. 2 white buck produced 26 young with coats indistinguishable from those of the wild grey. In the reverse cross, No. 3 white doe mated with No. 4 yellow-grey buck, gave 16 young, all with wild grey coats. One individual (No. 7) from the latter mating had, when young, rather more yellow on the chest and flanks than the others; but after the second moult it became almost wild grey, like the rest. Further experiments recently carried out have given similar results: altogether 70 individuals have been raised by mating yellow-grey with white, and all have wild grey coats. The following table gives the results of the individual matings (YG = yellow-grey, W = white):—

TABLE 19.

Yellow-grey \times White (F₁).

Matings				Wild Grey
YG 1 \times W 2	26
W 3 \times YG 4	16
W 6 \times YG 4	8
YG 13 \times W 2	4
W 23 \times YG 25	16
Total	70

(b) *Second Generation (F₂).*

The greys of the first generation bred together, with one exception, proved to be hybrid greys containing recessive black, giving a mixture of greys and blacks, the exception giving all greys. 7 greys of the first generation were tested together, and of these 6 proved to be hybrids, giving both grey and black young, usually in the same litter: the remaining one has so far given no blacks, and presumably is a pure grey.

The pure grey doe (No. 7) mated with 2 hybrid greys containing latent black (Nos. 10 and 12) produced 22 grey young.

The 6 hybrid greys mated together produced 110 coloured young, of which 85 were greys and 25 were blacks.

The individual results were as follows:—No. 5 gave 8 greys and 5 blacks; No. 8, 22 G and 6 B; No. 9, 33 G and 10 B; No. 10, 59 G and 19 B; No. 11, 22 G and 4 B; and No. 12, 26 G and 6 B.

All the 7 individuals gave white as well as coloured offspring; but these have already been dealt with under albinism (Sect. 2, p. 176).

The following table gives the individual matings, with the numbers of greys and blacks in each litter:—

TABLE 20.

Hybrid Greys bred together (F_2).

Matings			Grey	Black
H 5×H 12	4	2
H 5×H 10	4	3
H 8×H 10	5	3
H 8×H 10	8	0
H 8×H 10	6	2
H 8×H 10	3	1
H 9×H 10	5	3
H 9×H 10	5	0
H 9×H 10	5	1
H 9×H 10	7	0
H 9×H 10	2	5
H 9×H 10	3	1
H 9×H 12	6	0
H 11×H 12	5	1
H 11×H 12	6	1
H 11×H 12	5	2
H 11×H 10	6	0
Total	85	25

The greys of the second generation had wild grey coats like their parents, a few individuals appeared to have rather more yellow and less black than the wild grey; but, curiously enough, not one was a true yellow-grey like the Belgian grand-parent. The blacks of the second generation had black coats with no trace of the yellow pigment of the grey parents; all appeared to be shaded more or less with the brown pigment which is always associated with black, especially when the coat is moulting.

The nest coat was jet-black, but, in common with other black rabbits, after the first moult a few white hairs appeared, chiefly on the back and loins; these apparently increase in number with each moult, and a few have already developed these white hairs to such an extent as to almost resemble the well-known "Silver Grey" breed of the fanciers ("Chinchilla" of Darwin). It is hardly necessary to say that the so-called "Silver Grey" has no resemblance whatever to the wild grey, being a pure black breed when young; afterwards a number of white hairs appear among the black, giving it that silvered appearance so much admired by fanciers. The black individuals were easily distinguished from the grey ones at birth, their pigmented skin being a shade darker and covering the whole body, unlike the greys, in which the ventral area is but little pigmented, being pink or flesh-coloured.

The hybrid greys of the first generation, mated back with one of the original whites, also gave a mixture of greys and blacks, but only a few were raised.

The matings were as follows:—H 5 × W 2 gave 6 greys and 3 blacks, and H 8 × W 2 gave 5 greys and 1 black.

(c) *Third Generation (F₃).*

The blacks of the second generation extracted from the hybrid greys of the first generation have, so far, bred true when mated with one another¹. 5 individuals tested together gave 16 young, all blacks with no trace of yellow pigment. The following were the matings: EB 20 × EB 28 gave 6 blacks; EB 33 × EB 28 gave 6 blacks; and EB 54 × EB 41 gave 4 blacks. (For further results showing the purity of the extracted blacks, see Table 22.)

One of the extracted blacks EB 28 was mated with the pure grey G 7, producing 7 grey young.

The same extracted black was also mated with a hybrid grey EH 35, producing 2 greys and 5 blacks.

The greys of the second generation have, so far as tested, proved to be of two kinds, pure and hybrid, the former giving all greys, and the latter a mixture of greys and blacks. Out of 9 greys tested, 8 have proved to be hybrids containing recessive black, each of the 8 gave a mixture of greys and blacks, and in all there were 48 young, of which 38 were greys and 10 were blacks.

¹ Excluding the albinos thrown, which have been already dealt with under Sect. 2, p. 176.

The matings were as follows:—

TABLE 21.

Hybrid Greys bred together (F_3).

Matings	Grey		Black
EH 29 \times H 10	4		1
EH 29 \times EH 27	4		1
EH 30 \times H 10	4		1
EH 30 \times H 10	5		2
EH 31 \times H 12	2		1
EH 31 \times EH 26	3		0
EH 32 \times H 12	5		0
EH 32 \times H 10	4		1
EH 35 \times EH 26	5		1
EH 42 \times EH 26	2		2
Total	38		10

The remaining grey has, so far as tested, proved to be a pure grey, giving 11 grey young when mated with a black and with 2 hybrid greys. The matings were:—EG 36 \times EB 28 giving 3 greys; EG 36 \times H 10 giving 4 greys; and EG 36 \times EH 26 giving 4 greys. As these numbers are few, it is possible that this individual may yet prove to be a hybrid grey containing recessive black, and further experiments are necessary before we can be quite sure that it is a pure grey, especially as all the other 8 greys tested proved to be hybrids.

Both the greys and blacks of the third generation had similar coats to those of the second generation, there being still no return to the original yellow-grey of the Belgian.

SUMMARY OF COAT-COLOUR RESULTS.

In the first generation (F_1) yellow-grey \times white gave all wild greys. In the second generation (F_2), with one exception, the F_1 greys proved to be hybrids containing recessive black, for, when bred together, they gave a mixture of greys and blacks in Mendelian proportions. In the third generation (F_3) the F_2 blacks have so far bred true when mated together; they are recessive to pure grey and give a mixture of greys and blacks when mated with hybrid greys. The F_2 greys so far appear to be of two kinds, pure and hybrid, and the hybrids bred together give a mixture of greys and blacks in Mendelian proportions. From the

Mendelian point of view the above results are what might have been expected had the original parents been grey \times black instead of yellow-grey \times white.

Two points therefore appear to demand consideration:—the appearance of the black character, and the disappearance of the yellow-grey character.

The Appearance of the Black Character.

The sudden appearance of the black character in the second generation was quite unexpected, as there had been no black individuals in the ancestry of either of the original parents—Belgian or Angora—for at least 8 generations and probably many more. The fact that these black individuals appeared in about the proportion of one-quarter and bred true at once was very significant from the Mendelian point of view. It suggested that the hybrid greys of the first generation were giving off gametes, one-half of which contained the factor for black coat-colour. As these hybrid greys were bred from the yellow-grey Belgians crossed with the white Angora, it appeared that the black factor must have been introduced by one or the other of these parents, or by both.

That it was not introduced by both is clear from the absence of blacks in the first generation. That it was not introduced by the Belgian is equally clear from the fact that no blacks appeared when the Belgian was mated with a pure black, nor when the Belgians were mated together. From the Mendelian point of view, therefore, it would appear that the black factor must have been introduced by the white Angora. This may appear incredible, and yet, as the following experiments show, it seems to be the only interpretation of the facts.

Colour-factors latent¹ in Pure-bred Albinos.

The 2 albino Angoras originally used in the experiments were tested by mating them with the pure blacks of the second generation. No. 2 albino buck mated with 4 black does gave 16 black young. No. 3 albino doe mated with a black buck gave 11 young, of which 5 were black and 6 were grey. These results are in accordance with the

¹ To prevent misconception it should be stated that the colour-factors present in albinos are "*latent*" in the sense that their influence is not evident until some other ingredient, found in a pigmented individual, is added to them. When the precise nature of pigmentation is determined, it may be possible to substitute a more precise term. (Cf. Cuénot, 1903.)

conception that No. 2 albino gave off gametes, all of which carried the black factor, while No. 3 albino gave off gametes, some of which carried the black factor and others the grey factor.

To test the matter still further, No. 2 albino was mated with 5 grey hybrids known to contain recessive black, producing 38 coloured young, of which 21 were greys and 17 were blacks. If, as conceived, No. 2 albino was carrying latent black simply, the Mendelian expectation in this mating is 19 greys and 19 blacks. Again, No. 3 albino was mated with 2 grey hybrids known to contain recessive black, producing 7 coloured young, of which 5 were greys and 2 were blacks. These numbers are few, but if, as conceived, No. 3 albino was carrying both latent grey and latent black factors, the Mendelian expectation for 8 young is 6 greys and 2 blacks. This conception also explains certain facts in regard to the gametic constitution of the individuals of the first generation which are otherwise obscure. It will be remembered that while all the greys of the first generation by the No. 2 albino were hybrids containing recessive black, yet one individual grey (No. 7) out of No. 3 albino was a pure grey containing no black. The above conception that No. 2 albino gave off all black gametes, while No. 3 albino gave off both grey gametes and black gametes would explain the above facts, which were previously obscure.

In order to test whether these latent factors in albinos were subject to Mendelian segregation in simple albino matings, the No. 3 albino doe, apparently carrying grey and black, was mated with No. 2 albino buck, apparently carrying black only. 14 young were produced, all albinos, of course, with no trace of pigment. 2 of these young were tested with pure blacks and have so far given the following results:—

No. 23 albino doe mated with a pure black gave 5 blacks and 1 grey. No. 24 albino buck mated with a pure black gave 3 blacks: mated with a grey hybrid containing recessive black gave 6 blacks and 1 grey.

Although these results are few in number, yet it seems certain that No. 23 albino is carrying both grey and black, while No. 24 is apparently carrying black only.

The Mendelian expectation for albino (gr.-bl.) \times albino (bl.) is 1 albino (gr.-bl.) and 1 albino (bl.), which is apparently the result. The fact that in this case father and son are apparently carrying black only, while mother and daughter are apparently carrying grey and black, may be but a coincidence.

All the above results with pure-bred albinos are in accordance with the conception that albinos give off gametes carrying certain colour-

factors which remain latent until the albino is crossed with a pigmented individual, and yet, during their latency, obey the Mendelian laws of segregation and gametic purity. Further support is given to this conception by the results of the following experiments with extracted albinos.

Colour-factors latent in Extracted Albinos.

7 extracted albinos were tested for latent colour-factors, and of these, 2 apparently carried black only, while 5 apparently carried both grey and black. No. 14 albino buck mated with 2 pure blacks gave 6 blacks: mated with 2 grey hybrids containing recessive black it gave 3 greys and 5 blacks.

No. 45 albino doe mated with two pure blacks gave 9 blacks. These two albinos, which were apparently carrying black only, were extracted from No. 5 grey hybrid containing black, mated with No. 2 albino apparently carrying black, and are interesting as showing that albinos apparently carrying black only can be extracted from greys provided that the latter also contain black. No. 15 albino doe mated with 2 pure blacks gave 5 greys and 7 blacks; this albino was extracted out of No. 8 grey (bl.) \times No. 2 albino (bl.).

No. 16 albino doe mated with a pure black gave 7 greys and 5 blacks; this albino was extracted out of No. 7 pure grey \times No. 2 albino (bl.).

This case is interesting as showing that an albino extracted out of a pure grey does not necessarily carry grey only, the result depends upon both parents.

No. 34 albino doe mated with a pure black gave 4 greys and 4 blacks; this albino was extracted out of No. 11 grey (bl.) \times No. 12 grey (bl.).

No. 38 albino buck mated with a pure black gave 3 greys and 2 blacks.

No. 39 albino doe mated with two pure blacks gave 6 greys and 4 blacks.

The last two albinos were extracted from No. 7 pure grey \times No. 10 grey (bl.).

The three following tables give the individual matings in the testing of the pure-bred and extracted albinos for their latent colour-factors.

4 albinos apparently carrying black only mated with 7 pure blacks gave 34 black young, in accordance with the Mendelian expectation. These 34 blacks may therefore be added to the 16 already recorded

Purity of Extracted Blacks

under extracted blacks bred together (p. 193) making 50 in all, and will serve as a further illustration of the purity of the black recessives.

TABLE 22.

Albino (black) \times Black.				Grey	Black
Matings					
EB 19 \times A 2	0	2
EB 19 \times EA 14	0	3
EB 20 \times A 2	0	3
EB 21 \times A 2	0	4
EB 21 \times A 2	0	2
EB 21 \times EA 14	0	3
EB 33 \times A 24	0	3
EA 45 \times EB 28	0	5
EA 45 \times B 61	0	4
B 52 \times A 2	0	5
Total	0	34

7 albinos apparently carrying both grey and black mated with 5 pure blacks gave 64 young, of which 32 were greys and 32 were blacks, which is exactly the Mendelian expectation.

TABLE 23.

Albinos (grey and black) \times Black.				Grey	Black
Matings					
A 3 \times B 51	3	3
A 3 \times B 51	3	2
A 23 \times EB 28	1	5
EA 15 \times EB 28	2	2
EA 15 \times B 51	3	5
EA 16 \times EB 28	3	3
EA 16 \times EB 28	4	2
EA 34 \times B 49	4	4
EB 21 \times EA 38	3	2
EA 39 \times EB 41	2	0
EA 39 \times B 51	0	2
EA 39 \times B 51	4	2
Total	32	32

3 albinos, apparently carrying black only, mated with 6 grey hybrids containing black, gave 53 young, of which 25 were grey and 28 were black; the Mendelian expectation for 54 young being 27 greys and 27 blacks.

The results of the last table and this may also be added to the results given previously under hybrid greys mated with extracted blacks, giving in all 124 young, of which 59 were greys and 65 were blacks. The Mendelian expectation is 62 greys and 62 blacks (see p. 193).

TABLE 24.

Albino (black) × Grey (black).

Matings				Grey	Black
H 5 × A 2	2	0
H 5 × A 2	1	3
H 5 × A 2	3	0
H 8 × A 2	5	1
EH 17 × A 2	2	0
EH 17 × A 2	1	4
EH 18 × A 2	0	2
EH 18 × A 2	0	2
EH 18 × A 2	0	1
EH 18 × A 2	3	1
EH 18 × EA 14	1	3
EH 32 × A 2	4	3
EH 44 × EA 14	2	2
EH 44 × A 24	1	6
Total	25	28

The above results point to the following conclusions:—

(1) That both pure-bred and extracted albinos carry in their gametes certain colour-factors.

(2) Some albinos give off gametes containing the black factor only, while others give off gametes containing black and gametes containing grey, on the average in equal numbers.

(3) These colour-factors remain latent when albinos are mated together, but become patent when the albinos are mated with normal individuals.

(4) These latent colour-factors appear to follow the ordinary Mendelian rules of segregation and gametic purity.

(5) That the black character, which appeared in the second generation of the hybrids between the yellow-grey Belgian and the white Angora, was introduced by the albino Angora.

These conclusions, arrived at from experiments with Rabbits, fully confirm those already obtained by Prof. Cuénot in his important experiments with Mice; and although of necessity my experiments have been carried out on somewhat different lines, yet the conclusions are

the same in principle, and in presenting them I wish to acknowledge my indebtedness to Prof. Cuénot and Mr Bateson for their useful suggestions. There is no doubt that the demonstration of the fact of latent colour-factors being carried by albinos is of great significance, and will help to throw light upon a large number of observations, contributed by many observers in both animals and plants, that hitherto have remained obscure.

The Disappearance of the Yellow-grey Character.

With regard to the disappearance of the original yellow-grey character of the Belgian in all the generations, a number of experiments are now in progress, which, it is hoped, will throw some light upon the matter as soon as completed¹.

(4) UNIFORM AND MARKED COAT.

In the original experiments the Belgian parents had a uniform or self-coloured coat, with no trace of white markings on the extremities. (The almost white ventral area may for this purpose be disregarded.)

This self-colour character breeds true, so far as my experiments go, and to my knowledge for at least 8 previous generations and probably many more.

The 2 pure self-coloured Belgians were mated with 2 albino Angoras, and each albino gave a different result.

No. 2 albino buck mated with No. 1 self-coloured doe produced 26 self-coloured young with no trace of white markings on the extremities.

No. 3 albino doe mated with No. 4 self-coloured buck produced 16 young, of which one only was self-coloured, all the others being more or less marked with white on the fore-feet, shoulders, breast, nose, and forehead.

These white markings, though variable in extent, increased in a definite direction. The slightest markings were either on the tip of a fore-paw or at the end of the nose; as the markings increased they invaded the whole fore-feet, legs, shoulders, and breast, while the nose-markings extended towards the forehead; in other words, the whole tendency of the markings was towards the Dutch markings, so well known to fanciers. No. 7 was self-coloured, while No. 10 had white

¹ So far it is not possible to suggest what is the meaning of the non-appearance of the Belgian coat-colour in F_2 and F_3 .

fore-feet, legs, right shoulder, and breast, being the most marked of all; the others might be said to consist of a series between Nos. 7 and 10.

As different results were obtained from the 2 albinos, it is necessary to consider the offspring of the 2 lines of descent separately, viz.:—The self-coloured line raised from the No. 2 albino, and the marked line raised from the No. 3 albino.

(a) *The Self-coloured Line.*

In the first generation all the offspring were self-coloured. In the second generation 3 of the selfs of the first generation bred together and with a pure self produced 37 young, of which 35 were selfs and 2 were slightly marked with white, having a few white hairs on the tip of the right paw. The matings were as follows:—

TABLE 25.

Self \times Self (F_2).

Matings				Self	Marked
S 1 \times S 12	11	0
S 5 \times S 12	5	1
S 11 \times S 12	19	1
Total	35	2

In the third generation 5 of the selfs of the second generation mated together and with 2 pure selfs produced 25 young, all self-coloured. The matings were as follows:—

TABLE 26.

Self \times Self (F_3).

Matings				Self	Marked
S 31 \times S 12	3	0
S 31 \times S 26	3	0
S 32 \times S 12	5	0
S 42 \times S 26	4	0
S 43 \times S 25	10	0
Total	25	0

In the self-coloured line therefore, with two slight exceptions, the selfs bred true for three generations, including 88 individuals, notwithstanding that all were originally bred from an albino.

(b) The Marked Line.

In the first generation all the offspring, except one, were more or less marked with white on the fore extremities. In the second generation, 4 of the individuals of the first generation bred together produced 67 young, of which 16 were selfs, 34 were slightly marked with white like the parents, and 17 had the true Dutch markings. The individual numbers were as follows:—No. 7 gave 5 selfs, 2 marked, and 6 Dutch; No. 8 gave 3 selfs, 9 marked, and 6 Dutch; No. 9 gave 8 selfs, 23 marked, and 5 Dutch. It will be noted that each individual gave all three kinds; that No. 7, the self-coloured exception, gave more than the average number of full Dutch-marked and also of selfs; that No. 9, the one most marked with white, gave less than the average number of Dutch-marked. The individual matings and details of each litter were as follows (S = self-coloured hybrid, M = marked hybrid):—

TABLE 27.

Hybrid Self and Marked \times Marked (F_2).

Matings			Self	Marked	Dutch
S 7 \times M 10	1	1	1
S 7 \times M 10	2	0	1
S 7 \times M 10	2	1	4
M 8 \times M 10	0	4	4
M 8 \times M 10	2	4	2
M 8 \times M 10	1	1	0
M 9 \times M 10	2	6	0
M 9 \times M 10	1	4	0
M 9 \times M 10	0	4	2
M 9 \times M 10	2	4	1
M 9 \times M 10	1	4	1
M 9 \times M 10	2	1	1
Total	16	34	17

In the third generation, 3 of the extracted selfs bred together and with a pure self produced 15 young, of which 14 were selfs and 1 was slightly marked with white on the tip of the left paw. The matings were as follows:—

TABLE 28.

Extracted Selfs \times Selfs (F_3).

Matings			Self	Marked	Dutch
ES 35 \times ES 26	6	0	0
ES 36 \times ES 26	3	1	0
ES 36 \times S 47	5	0	0
Total	14	1	0

4 of the extracted Dutch bred together have so far given 10 young, all Dutch-marked. The matings were:—ED 53 \times ED 37 gave 6 Dutch, and ED 54 \times ED 41 gave 4 Dutch. 3 of the extracted marked individuals bred together and with hybrids gave 17 young, of which 3 were selfs, 12 were marked, and 2 were Dutch. The matings were:—EM 29 \times M 10 gave 0 selfs, 4 marked, and 1 Dutch; EM 29 \times EM 27 gave 1 self, 3 marked, and 1 Dutch; S 7 \times EM 28 gave 2 selfs, 5 marked, and 0 Dutch.

The Appearance of the Dutch Markings.

The appearance of the true Dutch markings in the second generation of the marked line only was as interesting as it was unexpected, especially as there had been no Dutch-marked individual in the ancestry of either the original self-coloured Belgian or the white Angora for at least 8 generations, and probably many more. The fact that these Dutch-marked individuals appeared in about the proportion of one quarter, and bred true at once, was very significant. From the Mendelian point of view, the results pointed to the conclusion that No. 3 albino Angora gave off gametes carrying the factor for Dutch markings, and that these gametes, uniting with the pure self gametes of No. 4 self-coloured Belgian, gave rise to the slightly marked hybrids of the first generation. Ordinary Mendelian segregation apparently took place in the gametes of these intermediate hybrids, giving rise to gametes for self-colour and gametes for Dutch markings in about equal numbers, with the result that in the second generation there were one quarter pure self, one half hybrid marked, and one quarter pure Dutch. In order to test this conception experimentally, a pure self-coloured doe (No. 46) was mated with a pure Dutch buck (No. 51), giving 5 young all slightly marked with white, like the marked hybrids of the first generation between the original albino No. 3 and the self-coloured No. 4.

No. 3 albino was then mated with the same pure Dutch buck (No. 51), giving 11 young, all of which had the true Dutch markings; showing that this albino was indeed giving off gametes, carrying the factor for Dutch markings only.

The other albino No. 2 (which mated with the self-coloured No. 1 gave the self line) was mated with a pure Dutch-marked doe (No. 52, bred out of the same litter as No. 51), giving 5 young, all slightly marked with white, and none with the full Dutch markings; showing that this albino was giving off gametes carrying the factor for self-colour only.

The above results go to show that pure-bred albinos carry the latent factors for self-colour and for Dutch markings.

The extracted albinos were also tested to some extent; and, so far as the experiments go, it appears that they also carry the latent factors for self-colour and Dutch markings.

Thus in the self line, 3 extracted albinos, Nos. 14, 34, and 45, so far as tested, appear to carry the self factor only, for mated with pure selfs they gave 16 young, all selfs, and mated with pure Dutch they gave 6 young, all slightly marked.

In the marked line, No. 39, extracted albino, appears to carry the self factor only, for mated with a pure Dutch it gave 10 young, all slightly marked; while the 2 extracted albinos, Nos. 15 and 16, appear to carry both the self and Dutch factors, for mated with pure selfs they gave 7 selfs and 3 slightly marked, and mated with pure Dutch they gave 10 Dutch and 9 marked.

So far as they go, therefore, the above results point to the following conclusions:—

(1) That both pure-bred and extracted albinos may carry the factors for self-colour and Dutch markings.

(2) Some of the albinos carry the self factors, others the Dutch factor only, and others, again, both the self and Dutch factors.

(3) The factors for coat-pattern remain latent when albinos are mated together, but become patent when the albinos are mated with normal individuals.

(4) The coat-pattern characters—unlike the previous characters dealt with—are neither dominant nor recessive towards one another, but when crossed give intermediate hybrids in the first generation. In the second and third generations, however, these characters appear to follow the ordinary Mendelian rules of segregation and gametic purity.

(5) The Dutch markings, which made their appearance in the second generation of the Belgian-Angora cross, appear to have been introduced by one of the albino Angoras (No. 3) and not the other (No. 2).

(6) The Dutch-marked rabbit would appear, therefore, to be a distinct mutation, rather than a partial albino caused by imperfect segregation. Similarly, the slightly marked forms are to be regarded as variable hybrids between the Dutch-marked and the self-coloured, rather than the result of varying imperfections of segregation from albinism.

These conclusions, arrived at from experiments with Rabbits, in some respects appear to be similar to those already obtained by

Prof. Cuénot with Mice, while in other respects they seem to differ. Both results are in agreement so far, that the "panachure" in mice and the Dutch markings in rabbits are unit characters in heredity following the ordinary Mendelian rules of segregation and gametic purity. Both agree, too, in the conclusion that these factors appear to be carried by albinos in a latent state.

The "panachure" in mice, however, seems to differ from the Dutch markings in rabbits, in so far that it appears to be completely recessive to self-colour or uniform coat; while, on the other hand, the Dutch markings, so far as observed, are neither recessive nor dominant to self-colour, giving variable hybrids, the majority of which have white markings tending towards Dutch markings. Occasionally, however, self-coloured hybrids appear, but, so far, no true Dutch-marked.

Another apparent difference between the "panachure" in mice and the Dutch markings in rabbits is that the latter seem to be more definite in character, with the pigment more localised than in the variable spotted mice. Further experiments with Dutch rabbits are now in progress in order to work out, if possible, some of these interesting details.

As will be seen from the list of references, the literature relating to the heredity of coat-colour in mice has been very extensive during the past two years, and space will not allow any detailed references to the important experiments of Cuénot, Darbishire, and Allen, and the valuable work of Bateson and Castle in the Mendelian interpretation of present and past records. Judging from my experience with rabbits, I am inclined to think that most, if not all, of the various complications and difficulties met with in the various experiments with mice may be interpreted by means of the simple Mendelian principles (bearing in mind the important results gained by Cuénot, in regard to the carrying of latent factors by albinos) without recourse to such interesting though complicated conceptions as mosaic gametes and resolution of compound characters.

SUMMARY.

Experiments in crossing Belgian rabbits with albino Angoras, and the subsequent interbreeding of the hybrids, have demonstrated the existence of 4 pairs of unit characters, viz.:—(1) Short and Angora coat; (2) Normality and albinism; (3) Grey and black coat; (4) Self-colour and Dutch markings. Each of these pairs is inherited independently of the other, so that all kinds of combinations occur among the offspring (see Table 29, p. 200).

The first two pairs of unit characters, short and Angora coat, normality and albinism, have been fully investigated, and in their heredity are found to follow Mendel's original *Pisum* type in regard to dominance, segregation, and gametic purity.

Short and Angora coat.—The Angora coat is recessive to short coat in the first generation, segregates in Mendelian proportions in the second generation, and breeds true in the third generation, notwithstanding its dominant short-coated ancestry.

The short coat is dominant over Angora coat in the first generation, and segregates in Mendelian proportions into two breeding forms in the second generation—pure and hybrid.

The pure form breeds true in the third generation, notwithstanding its Angora ancestry, while the hybrid form gives a mixture of shorts and Angoras in Mendelian proportions. Owing to dominance, the pure and hybrid shorts are indistinguishable in appearance, and can only be determined definitely by experimental breeding.

Normality and Albinism.—Albinism is recessive to normality in the first generation, segregates in Mendelian proportions in the second generation, and breeds true in the third generation, notwithstanding its dominant normal ancestry.

Normality is dominant over albinism in the first generation, and segregates in Mendelian proportions into two breeding forms in the second generation—pure and hybrid.

The pure form breeds true in the third generation, notwithstanding its albino ancestry, while the hybrid form gives a mixture of normals and albinos in Mendelian proportions. Owing to dominance, the pure and hybrid normals are indistinguishable in appearance, and can only be determined definitely by experimental breeding.

The investigation of the two remaining pairs of unit characters, grey and black coat, self-colour and Dutch markings, is not yet completed. So far as the experiments go, however, the following results appear:—

Grey and black coat.—Black is recessive to grey in the first generation, segregates in Mendelian proportions in the second generation, and breeds true in the third generation, notwithstanding its grey ancestry.

Grey is dominant over black in the first generation, and appears to segregate into two breeding forms in the second generation—pure and hybrid.

The apparently pure grey has so far bred true in the third genera-

tion, but the numbers are not yet sufficient to test the matter definitely. The hybrid greys give a mixture of greys and blacks in Mendelian proportions. Owing to dominance, the pure and hybrid greys are indistinguishable in appearance, and can only be determined definitely by experimental breeding.

In regard to the greys, an interesting complication was observed. The original grey used was a pure yellow-grey, containing more yellow pigment and less black than the ordinary wild grey. The greys of the first, second, and third generations were all wild greys, and, so far, there has been no return to the original pure yellow-grey.

Self-colour and Dutch markings.—So far as the experiments go, these characters appear to be neither dominant nor recessive to one another, but give variable intermediate marked hybrids in the first generation. Segregation into the three forms in Mendelian proportions, however, takes place in the second generation, and, so far, the extracted self-coloured and Dutch-marked forms have bred true in the third generation, while the intermediate marked hybrids give the three forms again in accordance with the Mendelian principles.

Latent factors in Albinos.—With regard to simple albinism, albinos of any ancestry so far breed true, the factor for normality being apparently eliminated in accordance with the Mendelian principles.

With regard to characters other than albinism, *but compatible with it*, such as short and Angora coat, these are carried by albinos in either a patent or recessive state. With regard to characters other than albinism, *but incompatible with it*, such as grey and black coat, self-colour and Dutch markings, these are also apparently carried by albinos, but in a latent state only.

Grey and black coat.—Albinos of the same ancestry extracted from hybrid greys, containing recessive black, so far appear to be of two kinds, viz.:—albinos carrying black, and albinos carrying grey and black.

Pure-bred albinos, with all albino ancestors for at least eight generations, and probably many more, so far appear to be of the same two kinds.

Experiments have not yet been carried out to test whether certain albinos carry grey only.

Self-colour and Dutch markings.—Albinos extracted from self-coloured parents appear to carry the latent factor for self-colour only, while albinos extracted from marked hybrids containing the self and Dutch factors appear to be of two kinds, viz.:—albinos carrying self-colour, and albinos carrying self and Dutch.

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Experiments have not yet been carried out to test whether extracted albinos carry Dutch only.

Pure-bred albinos with all albino ancestors for at least eight generations, and probably many more, so far appear to be of the three kinds, viz.:—albinos carrying self only, albinos carrying Dutch only, and albinos carrying both self and Dutch. All these latent factors for coat-colour and coat-pattern apparently carried by albinos do not become patent until the albino is bred with a normal or coloured form, presumably because they are incompatible with albinism. Nevertheless, in their latency, they appear to segregate gametically in albino matings as in normal matings, following the ordinary Mendelian rules of segregation and gametic purity.

These results confirm, and extend to rabbits, results already obtained by Prof. Cuénot in mice, though it would appear that the heredity of Dutch markings in rabbits differs in some respects from that of the "panachure" in mice.

Mendelian Analysis of individual Rabbits used in the Experiments.

The following table gives a list of 45 individual rabbits that have been analysed in these experiments in accordance with the Mendelian principles. First is given the Stud No. of the individual, the sex, the parentage, and the somatic characters somewhat abbreviated. Underneath is given the gametic constitution of the individual as determined in these experiments, the gametic factors being expressed in the same terms as the somatic characters above.

TABLE 29.

No. 1.	♀ (Pure Belgian): Short, normal, grey, self. GAMETES: <i>Short, normal, grey, self.</i>
No. 2.	♂ (Pure Angora): Angora, albino, white. GAMETES: <i>Angora, albino, black, self.</i>
No. 3.	♀ (Pure Angora): Angora, albino, white. GAMETES: <i>Angora, albino, grey & black, Dutch.</i>
No. 4.	♂ (Pure Belgian): Short, normal, grey, self. GAMETES: <i>Short, normal, grey, self.</i>
No. 5.	♀ (1 × 2): Short, normal, grey, self. GAMETES: <i>Short & Angora, normal & albino, grey & black, self.</i>
No. 7.	♀ (3 × 4): Short, normal, grey, self. GAMETES: <i>Short & Angora, normal & albino, grey, self & Dutch.</i>
No. 8.	♀ (3 × 4): Short, normal, grey, marked. GAMETES: <i>Short & Angora, normal & albino, grey & black, self & Dutch.</i>

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- No. 9. ♀ (3×4): Short, normal, grey, marked.
GAMETES: *Short & Angora, normal & albino, grey & black, self & Dutch.*
- No. 10. ♂ (3×4): Short, normal, grey, marked.
GAMETES: *Short & Angora, normal & albino, grey & black, self & Dutch.*
- No. 11. ♀ (1×2): Short, normal, grey, self.
GAMETES: *Short & Angora, normal & albino, grey & black, self.*
- No. 12. ♂ (1×2): Short, normal, grey, self.
GAMETES: *Short & Angora, normal & albino, grey & black, self.*
- No. 14. ♂ (5×2): Short, albino, white.
GAMETES: *Short & Angora, albino, black, self.*
- No. 15. ♀ (8×2): Angora, albino, white.
GAMETES: *Angora, albino, grey & black, self & Dutch.*
- No. 16. ♀ (7×2): Angora, albino, white.
GAMETES: *Angora, albino, grey & black, self & Dutch.*
- No. 17. ♀ (7×2): Short, normal, grey, self.
GAMETES: *Short & Angora, normal & albino, grey & black, self.*
- No. 18. ♀ (7×2): Short, normal, grey, self.
GAMETES: *Short & Angora, normal & albino, grey & black, self.*
- No. 19. ♀ (5×2): Short, normal, black, self.
GAMETES: *Short & Angora, normal & albino, black, self.*
- No. 20. ♀ (5×2): Angora, normal, black, marked.
GAMETES: *Angora, normal & albino, black, self.*
- No. 21. ♀ (5×2): Short, normal, black, marked.
GAMETES: *Short & Angora, normal & albino, black, self.*
- No. 22. ♀ (1×4): Short, normal, grey, self.
GAMETES: *Short, normal, grey, self.*
- No. 23. ♀ (3×2): Angora, albino, white.
GAMETES: *Angora, albino, grey & black, self & Dutch.*
- No. 24. ♂ (3×2): Angora, albino, white.
GAMETES: *Angora, albino, black, self & Dutch.*
- No. 25. ♂ (1×4): Short, normal, grey, self.
GAMETES: *Short, normal, grey, self.*
- No. 26. ♂ (11×12): Angora, normal, grey, self.
GAMETES: *Angora, normal & albino, grey & black, self.*
- No. 27. ♂ (9×10): Short, normal, grey, marked.
GAMETES: *Short & Angora, normal & albino, grey & black, self & Dutch.*
- No. 28. ♂ (9×10): Short, normal, black, marked.
GAMETES: *Short & Angora, normal, black, self & Dutch.*
- No. 29. ♀ (9×10): Short, normal, grey, marked.
GAMETES: *Short & Angora, normal & albino, grey & black, self & Dutch.*

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- No. 30. ♀ (11 × 12): Short, normal, grey, self.
GAMETES: *Short, normal, grey & black, self.*
- No. 31. ♀ (11 × 12): Short, normal, grey, self.
GAMETES: *Short & Angora, normal & albino, grey & black, self.*
- No. 32. ♀ (11 × 12): Short, normal, grey, self.
GAMETES: *Short, normal, grey & black, self.*
- No. 33. ♀ (11 × 12): Angora, normal, black, self.
GAMETES: *Angora, normal & albino, black, self.*
- No. 34. ♀ (11 × 12): Short, albino, white.
GAMETES: *Short, albino, grey & black, self.*
- No. 35. ♀ (9 × 10): Short, normal, grey, self.
GAMETES: *Short & Angora, normal, grey & black, self.*
- No. 36. ♀ (9 × 10): Short, normal, grey, self.
GAMETES: *Short, normal & albino, grey, self.*
- No. 37. ♂ (7 × 10): Angora, normal, grey, Dutch.
GAMETES: *Angora, normal & albino, grey, Dutch.*
- No. 38. ♂ (7 × 10): Short, albino, white.
GAMETES: *Short, albino, grey & black, self.*
- No. 39. ♀ (7 × 10): Short, albino, white.
GAMETES: *Short & Angora, grey & black, self.*
- No. 41. ♂ (3 × 10): Angora, normal, black, Dutch.
GAMETES: *Angora, normal & albino, black, Dutch.*
- No. 42. ♀ (8 × 2): Angora, normal, grey, self.
GAMETES: *Angora, normal & albino, grey & black, self.*
- No. 43. ♀ (1 × 12): Short, normal, grey, self.
GAMETES: *Short, normal, grey, self.*
- No. 44. ♀ (1 × 12): Short, normal, grey, self.
GAMETES: *Short & Angora, normal, grey & black, self.*
- No. 45. ♀ (5 × 2): Short, albino, white.
GAMETES: *Short & Angora, albino, black, self.*
- No. 50. ♀ (Pure Angora): Angora, albino, white.
GAMETES: *Angora, albino, grey & black, self.*
- No. 53. ♀ (7 × 10): Angora, normal, grey, Dutch.
GAMETES: *Angora, normal & albino, grey, Dutch.*
- No. 54. ♀ (9 × 10): Angora, normal, black, Dutch.
GAMETES: *Angora, normal & albino, black, Dutch.*

CONCLUSIONS.

A study of the somatic characters and gametic factors of the above individuals brings out the important fact that certain individuals, identical in appearance and with precisely the same ancestry, differ, in a regular and permanent manner, in their breeding potentialities (*e.g.* Nos. 35 and 36).

In such cases it is evident that neither the outward appearance of the individual nor a knowledge of its ancestry is a safe guide to its breeding potentialities (it is only in the case of recessive characters, of any ancestry, that the soma is a true guide), while, on the other hand, as the above experiments show, a knowledge of its gametic constitution and of the various dominances provides a sure guide.

Once the gametic formula of each individual has been determined by Mendelian analysis, the future results of any matings can be foreseen with accuracy, whereas a knowledge simply of the somatic characters of an individual and its ancestors is altogether unavailing.

The true measure of heredity therefore is neither the somatic character of the individual nor of its ancestors, but its gametic constitution, and, in our present state of knowledge, this can only be determined by experimental breeding on Mendelian lines.

REFERENCES.

- ALLEN, G. M. (1904). The Heredity of Coat-Colour in Mice. *Proc. Amer. Acad. Arts and Sci.* XL. pp. 61-163.
- BATESON, W. (1903). The Present State of Knowledge of Colour-heredity in Mice and Rats. *Proc. Zool. Soc. Lond.* II. pp. 71-99.
- CASTLE, W. E. (1903). The Heredity of Angora Coat in Mammals. *Science*, XVIII. pp. 760-1.
- CASTLE, W. E., AND ALLEN, G. M. (1903). The Heredity of Albinism. *Proc. Amer. Acad. Arts and Sci.* XXXVIII. pp. 603-622.
- CUÉNOT, L. (1902). La Loi de Mendel et l'Hérédité de la Pigmentation chez les Souris. *Arch. Zool. Exp.* (3) t. X. Notes et Revue, p. 27.
- (1903). La Loi de Mendel et l'Hérédité de la Pigmentation chez les Souris. *Compt. Rend. Paris*, CXXXIV. pp. 779-781.
- (1903). L'Hérédité de la Pigmentation chez les Souris. (2^{me} Note.) *Arch. Zool. Exp.* (4) t. I. Notes et Revue, p. 33.
- (1904). L'Hérédité de la Pigmentation chez les Souris. (3^{me} Note.) *Arch. Zool. Exp.* (4) t. II. Notes et Revue, p. 45.
- DARBISHIRE, A. D. (1904). On the Result of Crossing Japanese Waltzing with Albino Mice. *Biometrika*, III. pp. 1-51.
- (1904). On the Bearing of Mendelian Principles of Heredity on current Theories of the Origin of Species. *Mem. and Proc. Manch. Lit. and Phil. Soc.* XLVIII. pp. 1-19.
- WOODS, F. A. (1903). Mendel's Laws and some Records in Rabbit Breeding. *Biometrika*, II. pp. 299-306.

POSTSCRIPT¹.*The Mendelian Principles of Heredity.*

The classical experiments with Peas completed by Mendel in 1865 led him to the following conceptions of heredity².

A plant is composed of unit characters which are represented in the germ-cells, or gametes, by independent factors.

Pure breeding involves the union of *like* factors ($A \times A = AA$).

Cross breeding involves the union of *unlike* (but corresponding) factors ($A \times B = AB$).

Pure races give off gametes carrying the one factor concerned (AA gives off A_s simply).

Hybrid races give off two kinds of gametes, on the average in equal numbers, each carrying one of the factors concerned in the cross. *No gamete carries both* (AB gives off A_s and B_s in equal numbers, and no gamete carries A and B).

This is known as gametic segregation.

From this it follows that the offspring of the self-fertilised hybrids AB are of three kinds:—25 per cent. AA , 50 p.c. AB , and 25 p.c. BB .

The AA_s and BB_s , being gametically pure, breed true notwithstanding their AB origin.

This is known as gametic purity.

The AB_s , being hybrids, breed as such, gametic segregation again taking place.

When more than one pair of unit characters are concerned in the cross, the average result can be calculated on the above basis by the simple calculus of chance.

In his experiments Mendel encountered the phenomenon of dominance, *i.e.* when certain pairs of unit characters were crossed, one of the pair was always dominant over the other, which Mendel termed recessive: $A \times B = A(B)$.

This dominance of A over B in the soma caused the offspring of the self-fertilised hybrids to appear as $3A : 1B$. Analysis in the following generation, however, demonstrated their gametic formula to be $1AA : 2AB : 1BB$, in accordance with the Mendelian principles.

¹ Added by request of the Secretary of the Linnean Society.

² For English translation of Mendel's papers and further details see Bateson's *Mendel's Principles of Heredity* (Cambridge University Press, 1902).

XIII

EXPERIMENTAL STUDIES ON HEREDITY IN RABBITS¹

The following experiments with rabbits were undertaken two years ago, in order to determine whether the Mendelian principles of heredity might be applied to animals as well as to plants. Two pure-bred races were selected for crossing: the "Belgian Hare" and the White Angora. The so-called "Belgian Hare" is not a true hare in any respect, but is simply a rabbit bred to resemble the hare in form and colour. It has a short, yellow-grey, self-coloured coat, pigmented skin, dark eyes, and normal demeanour. The breed has been known in this country for more than a hundred years, and the individuals used in my experiments were from a local prize strain that had been bred true for eight generations at least, and probably many more.

The White Angora is a distinct albino breed with a pure white, long, fine coat, clear skin, devoid of pigment, pink eyes, and a curious swaying habit. This breed came originally from the East, where it has been cultivated as a distinct race probably for centuries. The individuals used in my experiments were from a local prize strain that had been bred true for many generations. A pair of each breed was crossed reciprocally, *i.e.* the Belgian doe was mated with the Angora buck, and the Angora doe with the Belgian buck (fig. 93).

In the first generation 70 hybrids were raised between the two races, 30 from the Belgian doe and 40 from the Angora doe. All alike had short coats, pigmented skin, dark eyes, normal demeanour, and grey coats like the common wild rabbit. In all these characters there was no difference in the two crosses, showing that the sire and dam had equal influence in the formation of the offspring. The resemblance of these hybrids to the wild rabbit, from which all the breeds have probably sprung, is very curious and interesting. It is no doubt what Darwin would have called a "reversion," but, as the sequel shows, it is not

¹ Read before Section "E" of the Leicester Literary and Philosophical Society, Jan. 23rd, 1905 and reprinted from *Trans. Leic. Lit. and Phil. Soc.* Vol. IX. Pt. 2 pp. 110-117 (1905).

a pure reversion but rather a reversionary resemblance, as it does not breed true. It may also be noted that the hybrids were much larger than the wild rabbit, and quite tame. When these grey hybrids of the first generation were bred together there was an "epidemic of variation" in the second generation consisting of no less than 14 somatic types (fig. 94).

A study of these from the Mendelian point of view shows that four distinct pairs of unit-characters are concerned, namely: Short and Angora coat, normality and albinism, grey and black coat colour, self-colour and Dutch markings. Each of these pairs of unit-characters is inherited independently of the other, so that all the possible combinations appear among the offspring, giving rise to apparently new types. In order to simplify the investigation, it is necessary to deal with each pair of unit-characters separately.

(1) SHORT AND ANGORA COAT.

The coat of the Belgian rabbit is made up of short, coarse fur, the longest hairs of which seldom exceed one inch. The Angora coat, on the other hand, consists of long, fine wool, the hairs of which often exceed six inches. Both kinds of coat bred true when mated with their own kind. When crossed, short coat was always dominant over Angora coat, which was recessive. In appearance, the hybrid short coat is practically indistinguishable from that of the pure short. To the touch, however, the hybrid coat seems to be softer and rather longer than that of the pure short, but the Angora influence is so slight that if one did not know the parentage one would hardly suspect it. The hybrid shorts bred together gave in the second generation a mixture of shorts and Angoras in Mendelian proportions. Out of 70 young there were 53 shorts and 17 Angoras. The Mendelian expectation for 68 young is 51 shorts and 17 Angoras. The Angora coats of the second generation were indistinguishable from those of the pure Angoras, while the short coats were similar in appearance to those of the pure and hybrid shorts.

The extracted Angoras bred true when mated together in the third generation, notwithstanding their mixed ancestry.

The shorts proved to be of two kinds, pure and hybrid.

The pure shorts bred true in the third generation, notwithstanding their mixed ancestry.

The hybrid shorts mated together gave in the third generation a mixture of shorts and Angoras in Mendelian proportions.

The pure shorts were only to be distinguished with certainty from the hybrid shorts by experimental breeding.

These experiments show that the unit-characters short and Angora coat so far follow in their heredity the Mendelian type, *Pisum*.

(2) NORMALITY AND ALBINISM.

The normal Belgian rabbit has a pigmented skin, coloured coat, dark eyes and normal demeanour. The albino Angora has a clear skin, devoid of pigment, pure white coat, pink eyes, and a curious habit of swaying the head from side to side, while the remainder of the body is at rest. In these experiments all these qualities or characteristics of the albino are correlated and inherited as one unit-character, which, for convenience, may be simply called albinism as opposed to normality. Both the normal and albino characters bred true when mated with their own kind.

When crossed, normality was always dominant over albinism, which was recessive. In some cases there was no trace of the albino character in the appearance of the hybrids. In other cases, however, the hybrids were slightly marked with white on the fore extremities, but, as will be shown later, these white markings do not seem to be connected with simple albinism.

The hybrid normals bred together gave in the second generation a Mendelian mixture of normals and albinos. Out of 171 young there were 132 normals and 39 albinos. The Mendelian expectation for 172 young is 129 normals and 43 albinos.

The albinos of the second generation were indistinguishable from pure albinos, having a clear skin devoid of pigment, pure white coat, pink eyes, and the swaying habit.

The normals of the second generation were similar to the pure and hybrid normals, having a pigmented skin, coloured coat, dark eyes and normal demeanour. Most of them were self-coloured, some were slightly marked with white, and a few were marked like the pure Dutch rabbit. As will be shown later, these white markings have apparently no connection with simple albinism.

The extracted albinos bred true in the third generation when mated together, notwithstanding their mixed ancestry.

The normals proved to be of two kinds, pure and hybrid.

The pure normals bred true in the third generation, notwithstanding their mixed ancestry.

The hybrid normals bred together in the third generation gave a Mendelian mixture of normals and albinos. Out of 65 young there were 48 normals and 17 albinos.

The pure normals were only to be distinguished from the hybrid normals by experimental breeding. These experiments show that the unit-characters normality and albinism follow in their heredity the Mendelian type, *Pisum*.

(3) GREY AND BLACK COAT-COLOUR.

The yellow-grey coat of the Belgian rabbit contains two distinct pigments, yellow and black, in various dilutions, while a third pigment, brown or chocolate, is also found in close association with the black.

The distribution of these pigments and their dilutions is of a complicated nature, yet, nevertheless, the yellow-grey coat breeds true.

The pure white coat of the albino Angora contains no trace of pigment and also breeds true.

The hybrids all had grey coats like the wild rabbit. The wild-grey coat contains precisely the same pigments as the yellow-grey, the only difference being that the wild-grey contains more of the black pigment and less of the yellow than does the yellow-grey.

The grey hybrids bred together gave in the second generation a mixture of greys and blacks in Mendelian proportions. Out of 110 young there were 85 greys and 25 blacks.

The Mendelian expectation for 112 young is 84 greys and 28 blacks.

The blacks contained only the black and brown pigments with no trace of the yellow.

The greys contained, as usual, all three pigments, black, brown, and yellow, and all were of the wild-grey type, there being no return to the original yellow-grey.

The extracted blacks bred true in the third generation, when mated together, notwithstanding their mixed ancestry (excluding the albinos thrown, which have already been dealt with).

The greys proved to be of two kinds, pure and hybrid; the pure greys bred true in the third generation (excluding the albinos) while the hybrid greys gave a mixture of greys and blacks in Mendelian proportions.

The sudden appearance of the black character in the second generation was most interesting, as there had been no black individuals in the ancestry of either the Belgian or the Angora for at least eight genera-

tions, and probably many more. The fact that these black individuals appeared in Mendelian proportions, and bred true at once, was significant. From the Mendelian point of view, it is evident that the hybrid greys of the first generation were giving off gametes or gerin-cells, one half of which contained the factor for black coat-colour; *i.e.*, they were dominant greys containing recessive black. Now these hybrid greys were bred from the Belgian crossed with the albino, so that the black factor must have been introduced by one or the other of those parents or by both. That it was not introduced by both is clear from the absence of blacks in the first generation. That it was not introduced by the Belgian is equally clear from the fact that no blacks appeared when the Belgian was mated with a pure black, nor when the Belgians were mated together. From the Mendelian point of view, therefore, the black factor must have been introduced by the albino.

In order to test this conception experimentally, the two albinos used in the experiments were mated with pure blacks, with the result that one gave all blacks, while the other gave a mixture of greys and blacks in about equal numbers. From the Mendelian point of view, therefore, it would appear that one albino was carrying the latent factor for black coat-colour only, while the other was carrying latent factors for grey and black coat. To test the matter further, the albino carrying latent black only was mated with hybrid greys known to contain recessive black, and these gave a mixture of greys and blacks in Mendelian proportions.

These facts are in accordance with the conception that pure-bred albinos may carry latent factors for grey and black coat-colour, and that the black character which appeared in the second generation of the Belgian-Angora cross was introduced by the albino Angora. Further support is given to this conception by similar experiments with the extracted albinos.

Seven of these were tested with pure blacks, with the result that two were found to be carrying latent black only, while five were carrying latent factors for grey and black. These results extend to rabbits the conclusions arrived at by Professor Cuénot, in his experiments with mice.

There is no doubt that the demonstration of the fact of latent colour factors being carried by albinos is of great significance, and will help to throw light on a large number of observations in plants and animals that hitherto have remained obscure.

(4) SELF-COLOUR AND DUTCH MARKINGS.

The Belgian parents had a uniform or self-coloured coat, with no trace of white markings on the fore extremities. The albino parents were, of course, without colour. Both kinds bred true. When crossed, the hybrids from one albino were all self-coloured, while those from the other albino were (with one exception) more or less marked with white on the fore-feet, shoulders, breast, nose and forehead. These white markings, though variable in extent, increased always in a definite direction towards the true Dutch markings, so well known to fanciers.

In the second generation the self-coloured individuals from the self-line bred true when mated together. The slightly marked individuals from the marked line, when bred together, give a mixture of selfs, slightly marked, and Dutch marked, in Mendelian proportions. Out of 67 young there were 16 selfs, 34 marked and 17 Dutch. The Mendelian expectation for 68 young is 17 selfs, 34 marked, and 17 Dutch.

In the third generation the selfs of the self-line again bred true. The selfs of the marked line also bred true, with one slight exception.

The extracted Dutch of the marked line bred true when mated together, while the slightly marked ones bred together gave all three kinds again, self, marked, and Dutch, in Mendelian proportions. From the Mendelian point of view, these results point to the conclusion that the albino which gave the self-line was carrying the factor for self-colour; while the albino which gave the marked line was carrying the factor for Dutch markings. Confirming this conception, experiments in crossing pure selfs with pure Dutch gave slightly marked hybrids like those raised from the albino carrying Dutch and the self Belgian.

Again, the albino carrying Dutch, mated with a pure Dutch, gave all Dutch-marked young, while the albino carrying self-colour mated with a pure Dutch gave all slightly marked young. These results show that pure-bred albinos may carry latent factors for coat-pattern, as well as for coat-colour, and that the Dutch markings which appeared in the second generation of the Belgian-Angora cross were introduced by one of the albino Angoras and not the other. Experiments with the extracted albinos also confirm this conclusion.

The factors for coat-pattern like those for coat-colour remain latent in albino matings (presumably because they are incompatible with albinism) but become active when the albino is mated with a normal,

pigmented individual. Both kinds of factors appear to follow the ordinary Mendelian rules of segregation and gametic purity during their latency. It will be observed that the two coat-pattern characters, self-colour and Dutch markings—unlike the other Mendelian characters dealt with—are neither dominant nor recessive, but, when crossed, give, in the first generation, variable and intermediate hybrids.

In the second and third generations, however, these characters follow the ordinary Mendelian rules of segregation and gametic purity.

The Dutch-marked rabbit would appear, therefore, to be a distinct mutation rather than a partial albino, as usually supposed. Similarly, the slightly marked forms are to be regarded as variable hybrids between the Dutch-marked and the self-coloured, rather than variable, partial albinos.

CONCLUSIONS.

In these experiments, the gametic or germinal constitution of 45 individual rabbits of known ancestry has been determined for four pairs of unit-characters. A study of this material shows that except in the case of recessive characters, the outward appearance of an individual is no safe guide to its breeding potentialities. Further, that in all kinds of characters, a knowledge of the ancestry is equally unavailing as a guide to heredity. As a simple illustration of this, two short, grey rabbits of the second generation of the Belgian-Angora cross (Nos. 35 and 36) may be taken. In outward appearance they are exactly alike. Their ancestry is identical, both being from the same litter. Yet, notwithstanding this, their germinal constitution is quite different, and, consequently, each differs from the other in its heredity, uniformly and permanently.

The somatic formula for both may be written $S + N + G$, *i.e.* short, normal, and grey. The gametic formulæ were, however, found to be as follows: (A = Angora, B = Black, W = Albino) No. 35 = $SA + N + GB$ (containing "black" and "Angora" recessive). No. 36 = $S + NW + G$ (containing "albino" recessive). These two rabbits are representatives of the 81 possible gametic types, each of which differs from the other in germinal constitution and heredity, and yet, one and all have identical ancestry. From these facts it is evident that the true measure of

heredity is neither the outward appearance of the individual nor its ancestry, but its germinal constitution.

In the present state of knowledge this can only be determined by experimental breeding on Mendelian lines. Of the 14 somatic types that appeared in the second generation, 10 bred true to type at once (*i.e.* if the pure forms were selected and the hybrid ones discarded), and of these eight were new races (at least so far as they had not appeared in the ancestry for at least nine and probably many more generations). All the eight races, however, resembled the forms known to fanciers as: "Silver-greys," "Black Dutch," "Grey Dutch," "Black Angoras," "Black and White Angoras," "Grey Angoras," "Grey and White Angoras," and "Polish." The pure white "Angora" parent was also repeated, but, curiously enough, the true "Belgian Hare" did not reappear, being apparently replaced by a large, tame rabbit with the wild grey colour. In all, 10 pure races were obtained in the second generation by crossing the two pure races. These 10 races, notwithstanding their mixed ancestry, bred true at once without any continued selection or need for fixation. It appears, therefore, that the fixation of a race depends solely on the selection of the pure form and the discarding of the hybrid. If a race be selected at sight, without experimental testing of its germinal constitution, the chances are that a hybrid form will be selected, as the ratio of pure forms to hybrids is as 1 : 2.

In such a case, after a generation of selection, the breeder is no nearer fixation than when he started. This might go on for a number of generations until the pure form was by chance selected, then the breed would be fixed at once. This explains how it is that some races have been fixed quickly and others slowly. In the case of certain breeds, such as the Blue Andalusian fowl, fixation apparently never takes place, simply because the blue character of the breed is a Mendelian hybrid. If a pair of blue Andalusians (with a blue pedigree for any number of generations) be mated together, the result will be a Mendelian mixture of 25 % splashed whites, 25 % blacks and 50 % blues.

The splashed whites, bred together, breed true at once, notwithstanding their blue ancestry. The blacks also breed true though blue bred. The blues give all three colours again, though blue bred. But if the splashed whites be mated with the blacks, the result is all blues. It is obvious, therefore, that the blue Andalusian is a hybrid breed of black and splashed white and the blue character being a Mendelian hybrid will never breed true. In such cases, careful selection is of no

avail, and mere pedigree is a delusion and a snare, though the whole of the facts are in simple harmony with the Mendelian principles of heredity.

It will be perceived that the recent discoveries in heredity have far-reaching consequences. In face of the new facts, it is evident that current ideas of selection and ancestry will have to be considerably revised, or at any rate, regarded from a different standpoint

XIV

EXPERIMENTS WITH POULTRY¹

These experiments were designed in 1901, to test the Mendelian principles of heredity. Four pure breeds were selected for experimental crossing, viz., White Leghorn, Houdan, Black Hamburg, and Buff Cochin.

PURE BREEDS (P₁).

White Leghorn.—The chief characters of the breed are, clear white plumage, large single comb, four toes on each foot and yellow shanks quite free from feathers. The white plumage often acquires a yellowish tint when exposed to the sun, but the birds always moult out clear white. The down of the chick is at first yellowish white, afterwards becoming clear white. The large single comb, erect in the cock, and falling over to one side in the hen, consists of a single lobe, extending beyond the back of the head, with four to five deep and even serrations. The deep yellow shanks become lighter with age. The hens lay white eggs, as a rule, and do not "sit."

Houdan.—The chief characters of the breed are, black plumage ticked or mottled with white, large crest, beard, and muffling, leaf comb, 5 toes on each foot, white shanks spotted with blue-black, usually free from feathers. This breed has an abnormal protuberance of the skull with cavernous nostrils, both of which appear to be correlated with the large crest². The plumage is a dull blue-black shaded with brown; the white markings are irregular in size and distribution, varying from a few white ticks in the dark birds to clear white feathers in the flights and crest of the light ones. The down of the chick is clear black above with white head and underparts irregularly mottled with black. The leaf comb is an irregular structure consisting of 2 single serrated lobes spread out somewhat like the leaves of an open book, and joined at the base by a mulberry-shaped process; it is always

¹ Reprinted from *Reports to the Evolution Committee of the Royal Society*, II. pp. 131-154 (1905).

² Cf. Darwin, *Animals and Plants*, I. p. 275, 2nd. ed. 1893.

large in the cock and small in the hen, and varies considerably in detail in individual birds, though unmistakably different from any other kind of comb. The ideal leaf comb of the fancier has been likened to a butterfly with open wings. The extra-toe is usually a distinct digit, curving gently upwards, sometimes it is imperfect and even joined to the hallux. The pigmentation of the white shanks is variable, in some cases there are a few small spots, while in others the spots are so numerous and suffused that the shanks appear to be blue-black rather than white. The shanks are usually free from feathers, but sometimes birds appear with a few traces of feathers on the upper part of the shanks. The crest varies in size in individual birds. The hens lay white eggs and do not "sit."

Black Hamburg.—The chief characters of the breed are, black plumage, rose comb, 4 toes on each foot, and blue-black shanks, quite free from feathers. The black plumage has a lustrous green sheen. The down of the chick is clear black above with whitish throat and underparts, but the white disappears with maturity, leaving the bird clear black. The rose comb has a flat surface covered with a large number of small points, it is squared in front, gradually tapering backwards to a long spike or peak. The breed is small in size, close-feathered, with a neat and active carriage. The hens lay pure white eggs and do not "sit."

*Buff Coch.*n.—The chief characters of the breed are, buff plumage, small single comb, 4 toes on each foot, and yellow shanks heavily feathered down to the toes. The buff plumage varies considerably in individual birds, and also with age; the shades range from lemon to cinnamon, some of the darker cocks having quite a red tinge in their hackles and saddle feathers; black or brown feathers in the tail, white feathers in the flights, and mealy or white speckled birds are often seen in the most carefully selected strains. The down of the chick varies from light to dark buff, shaded with creamy white. The small single comb is erect in both sexes and very small in the hen. The shank-feathering varies in length and number of feathers in individual birds. The hens lay dark brown eggs, and frequently want to "sit." The breed is large in size, with loose, fluffy feathers and heavy limbs.

The above observations were obtained by the personal examination of more than 2000 birds of the pure breeds concerned, and in the particular strains from which the stock birds, used in these experiments, were derived.

FIRST CROSSES (F_1).*Experiment 1.—White Leghorn ♀ × Houdan ♂.*

In 1902, 12 White Leghorn hens were mated with a dark Houdan cockerel; eggs from this pen produced 105 chicks with the following characters:—

COMB.—*Single ♀ × Leaf ♂* gave all with variable leaf combs; of these, 9 were apparently full leafs, and 96 were split leafs, having a single lobe in front split into two more or less concave lobes behind; there were no single combs.

DOWN.—*White ♀ × Black ♂* gave 94 whites and 11 blacks; of these 22 were apparently clear white, 72 white ticked with black, 1 black with white head, and 10 black, ticked with white. In each case the tickings were slight and inextensive, so that in the ground colour the distinction between white and black was marked and discontinuous. In the first plumage all except two of the clear whites developed black ticks, similar to those that were born ticked; the blacks developed into 6 blacks and 5 "cuckoos," 5 of the blacks were slightly ticked with white in the crest only, and in their plumage were indistinguishable from the Crève-cœur breed, the other black developed into a typical light Houdan; the 5 cuckoos were grey-white, barred with blue-black, with odd black or white feathers; both the blacks and the cuckoos were distinctly shaded with brown. Curiously enough the 6 blacks were all pullets and the 5 cuckoos all cockerels! (See p. 232.)

FEET.—*No-extra-toe ♀ × Extra-toe ♂* gave 103 with e.t., and 2 with no e.t.; of these, 23 had the e.t. apparently perfect on both feet, 70 had e.t. in all stages from the almost perfect e.t. down to the mere duplication of the nail, 6 had e.t. on one foot only, while 4 had 4 toes on each foot, but in each case the hallux was elongated with extra joints, all these various states indicating digital proliferation are counted as e.t. The 2 chicks with no e.t. were apparently normal with no trace of e.t.

SHANK FEATHERING.—*Clear ♀ × Clear ♂* gave 103 with clear shanks and 2 with a few traces of feathers on the upper part of the shanks; both the latter were cockerels, and one was also exceptional in having cuckoo plumage and no e.t.

SHANK COLOUR.—*Yellow ♀ × White ♂* gave all with white shanks, more or less pigmented with blue-black; the cockerels without exception had very little pigment, while the pullets, with 4 exceptions, had a

large amount, and at a distance appeared more blue than white in their shanks. There were no yellow shanks nor any tinged with yellow.

EGG COLOUR.—*White* ♀ × *White* ♂ gave all with white eggs.

CREST.—*Clear* ♀ × *Crested* ♂ gave all crested, but in every case the size of the crest, in both length and number of feathers, was reduced to about one-half.

BROODINESS.—*Non-Sitting* ♀ × *Non-Sitting* ♂ gave all non-sitters.

Experiment 2.—*White Leghorn* ♀ × *Black Hamburgh* ♂.

In 1903, 10 White Leghorn hens were mated with a Black Hamburgh cock; eggs from this pen produced 57 chicks with the following characters:—

COMB.—*Single* ♀ × *Rose* ♂ gave all rose combs with no trace of the single comb.

DOWN.—*White* ♀ × *Black* ♂ gave 49 whites and 8 blacks; of these, 1 was apparently clear white, 48 white ticked with black, and 8 black with whitish throats.

FEET.—*No-e.t.* ♀ × *No-e.t.* ♂ gave all with no trace of e.t.

SHANK FEATHERING.—*Clear* ♀ × *Clear* ♂ gave all clear with no trace of feathers. These chicks were not reared for the observation of their mature characters.

Experiment 3.—*White Leghorn* ♀ × *Buff Cochin* ♂.

In 1903, 12 White Leghorn hens were mated with a Buff Cochin cockerel; eggs from this pen produced 60 chicks with the following characters:—

COMB.—*Single* ♀ × *Single* ♂ gave all with single combs.

DOWN.—*White* ♀ × *Buff* ♂ gave 53 whites and 7 buffs; of these 2 were apparently clear white, 51 white patched with buff and brown, chiefly on the head, neck and breast (18 of these had also odd black ticks); the 7 buffs were all more or less patched white.

FEET.—*No-e.t.* ♀ × *No-e.t.* ♂ gave all with no trace of e.t.

SHANK FEATHERING.—*Clear* ♀ × *Feathered* ♂ gave all with feathered shanks, but in every case the length and number of feathers was reduced to about one-half.

Experiment 4.—*Black Hamburgh* ♀ × *Houdan* ♂.

In 1903, late in the season, one Black Hamburgh hen was mated with a light Houdan cockerel, and only 6 chicks were hatched, with the following characters:—

COMB.—*Rose* ♀ × *Leaf* ♂ gave all rose combs, but they were irregular,

inasmuch as the usual long peak of the pure rose was replaced by two shorter ones.

DOWN.—*Black* ♀ × *Black* ♂ gave all blacks with white heads.

FEET.—*No-e.t.* ♀ × *E.t.* ♂ gave all with e.t. on both feet.

SHANK FEATHERING.—*Clear* ♀ × *Clear* ♂ gave all clear shanks, with no trace of feathers.

Experiment 5.—Buff Cochín ♀ × Houdan ♂.

In 1903, late in the season, one Buff Cochín hen was mated with a light Houdan cockerel, and only 5 chicks were hatched, with the following characters:—

COMB.—*Single* ♀ × *Leaf* ♂ gave all with split leaf combs.

DOWN.—*Buff* ♀ × *Black* ♂ gave all blacks marked and shaded with brown and ticked with white.

FEET.—*No-e.t.* ♀ × *E.t.* ♂ gave 4 with e.t. on both feet and 1 with no e.t.

SHANK FEATHERING.—*Feathered* ♀ × *Clear* ♂ gave all with feathered shanks, but the length and number of feathers was reduced to about one-half.

Experiment 6.—Black Hamburgh × Buff Cochín.

In 1902, two Black Hamburgh pullets were mated with a Buff Cochín cockerel; eggs from this pen produced 84 chicks. At the same time one Buff Cochín pullet was mated with a Black Hamburgh cockerel; eggs from this pen produced 23 chicks. The offspring of these reversed matings had similar characters, so that all may be taken together, *i.e.*, 107, with the following characters:—

COMB.—*Rose* × *Single* gave all rose combs with no trace of single comb.

DOWN.—*Black* × *Buff* gave all blacks marked with brown; of these, 82 had brown heads only, and 25 had also the body shaded with brown. In the first plumage the two sexes were quite distinct. The cockerels had golden-brown hackles, red-brown saddles, black and brown tails and wings, buff-brown breast regularly spangled with black. The pullets were as dull and sober in colour as the cockerels were brilliant, being black intermixed with light and dark brown, with darker tails and heads and spangled breasts. It seems rather curious that a cross between two breeds, each of which has normally similar plumage in both sexes, should produce offspring in which the two sexes are so distinctly differentiated.

FEET.—*No-e.t.* × *No-e.t.* gave all with no trace of e.t.

SHANK FEATHERING.—*Clear* × *Feathered* gave all with feathered shanks, but in each the length and number of feathers was reduced to about one-half.

SHANK COLOUR.—*Blue* × *Yellow* gave all with light blue shanks with no trace of yellow.

CREST.—*Clear* × *Clear* gave all clear with no trace of crest.

EGG COLOUR.—*White* × *Brown* gave all with brown eggs of varied hue, none being so brown or so white as the parent breeds.

BROODINESS.—*Non-sitting* × *Sitting* gave all good sitters; all the pullets wanted to sit after laying about a dozen eggs, and all successfully hatched two lots of chicks in 1903, making excellent foster-mothers, having the strong incubating instinct of the Cochin combined with lightness of limb of the *Hamburgh*. The voice of the cross-bred cockerels was a ludicrous compromise between the hoarse prolonged crow of the Cochin and the shrill sharp crow of the *Hamburgh*. The cross-breds were intermediate in size, carriage and feathering.

In the foregoing first crosses, each of the six possible combinations of the four pure breeds has been effected, and in the one reverse cross tried (Experiment 6), no intrinsic differences could be detected in the offspring through the change of sex. Many different characters are concerned in the six matings, some are like, others are unlike. The matings of like characters in the first crosses (F_1), gave the same result as the like matings in the pure breeds (P_1). The matings of unlike characters in F_1 gave, generally, a definite dominance of one character over the other, e.g., in Experiment 1, white plumage mated with black gave nearly all whites; in Mendelian terms, white was dominant over black, which was recessive. A few exceptions occurred in which the normally recessive black was apparently dominant, e.g., in Experiment 1, a few were black instead of white. Among the hybrid dominants the dominance was clearly of two kinds, *complete* and *incomplete*. Complete dominance resembled the original Mendelian dominance in Peas, where no trace of the recessive character was found in the hybrid dominant, e.g., in Experiment 1, a few were clear white with no trace of black. Incomplete dominance occurred when the influence of the recessive character was manifest in the hybrid dominants in varying degrees, e.g., in Experiment 1, a large proportion were white ticked with black. The following table gives the total results of the first crosses (F_1), showing in (a) the names and numbers of the D and R characters that

occurred in the unlike matings $D \times R$, together with the respective numbers of the complete and incomplete dominants; and in (b) the numbers observed in the like matings $R \times R$.

TOTAL RESULTS OF FIRST CROSSES (F_1).(a) *Matings of Unlike Characters ($D \times R$).*

Expts.	Character	D	R	D	R	Com- plete	Incom- plete
						D	D
1, 5	Comb.....	<i>Leaf</i>	Single.....	110	0	9	101
2, 6	"	<i>Rose</i>	Single.....	164	0	164	0
4	"	<i>Rose</i>	Leaf	6	0	0	6
1, 2	Down	<i>White</i>	Black	143	19	23	120
3	"	<i>White</i>	Buff	53	7	2	51
5, 6	"	<i>Black</i>	Buff	113	0	0	113
1, 4, 5	Feet	<i>E.t.</i>	No e.t.	113	3	25	88
3, 5, 6	Shanks	<i>Feathered</i>	Clear	173	0	0	173
1	"	<i>White</i>	Yellow	105	0	105	0
6	"	<i>Blue</i>	Yellow	107	0	107	0
1	Crest	<i>Crested</i> ..	Clear	105	0	0	105
6	Eggs	<i>Brown</i>	White.....	31	0	0	31
6	Broodiness	<i>Sitting</i>	Non-sitting	31	0	31	0
Total.....				1254	29	466	788
Per cent. ...				97.7	2.2	36.3	61.4

(b) *Matings of Like Characters ($R \times R$).*

Expts.	R character	D	R
3	Single comb	0	60
4	Black down	0	6
2, 3, 6	No e.t.	0	224
1, 2, 4	Clear shanks ...	2	166
6	No crest	0	107
1	White eggs	0	53
1	Non-sitting	0	53
Total.....		2	669
Per cent. ...		0.2	99.7

The above table shows that out of the 1283 characters observed in the $D \times R$ mating of F_1 , 1254 (97.7 per cent.) were definitely dominant, the remaining 29 (2.2 per cent.) being apparently recessive. Of the 1254 dominants, 466 were apparently complete, while 788 were obviously incomplete. In Mendel's experiments with Peas, $D \times R$ in F_1 gave all complete dominants with no trace of R , but when the hybrid

dominants were bred together in F_2 , the R character re-appeared, proving that though not patent in F_1 , it was nevertheless latent, and that the hybrid dominants raised from $D \times R$, though apparently simple D's were in reality DR's. In these experiments with poultry it is obvious that the incomplete dominants are impure DR's, because they show the influence of the R character in F_1 , in some degree, however slight it may be; but further breeding in F_2 is required to show that the complete dominants are also impure DR's, and the following experiments show clearly that such is the case.

The Mendelian expectation from the mating $DR \times DR$ in F_2 is a proportion of 3 dominants to 1 recessive. The two following experiments give the results of two such matings, in several pairs of characters, in two distinct first crosses.

FIRST CROSSES BRED TOGETHER (F_2).

Experiment 7.—*Leghorn-Houdan* ♀ \times *Leghorn-Houdan* ♂.

In 1903, 12 pullets bred in Experiment 1 were mated with a cockerel bred in the same experiment, and with similar characters; eggs from this pen produced 226 chicks, with the following characters:—

COMB.—DR LEAF (*single*) ♀ \times DR LEAF (*single*) ♂ gave 165 leafs and 61 singles, or 2·7 D : 1 R; of these 67 were full leafs, 98 split leafs, 56 ordinary singles, and 5 singles with the hinder end somewhat thickened (cf. Experiment 1).

DOWN.—DR WHITE (*black*) ♀ \times DR WHITE (*black*) ♂ gave 171 whites and 55 blacks, or 3·1 D : 1 R. Of these, 111 were apparently clear white, 60 white ticked with black, 32 black with white heads, and 23 black ticked with white. A few only were reared, and these developed their first plumage as in the down, except that some of the clear whites developed black ticks, and some of the blacks ticked with white developed into "cuckoos" (cf. Experiment 1).

FEET.—DR 5 (4) ♀ \times DR 5 (4) ♂ gave 179 with e.t. and 47 with no e.t. or 3·8 D : 1 R. Of these, 167 had e.t. on both feet, 7 had e.t. on one foot only, 2 had e.t. on one foot and long hallux on the other, 1 had long hallux on both feet, 2 had six toes on each foot, and 47 had no trace of e.t. (cf. Experiment 1).

SHANK FEATHERING.—RR Clear ♀ \times RR Clear ♂ gave 219 clear, and 7 with feather traces, or 96·9 per cent. R (cf. Experiment 1).

Experiment 8.—Hamburgh-Cochin ♀ × Hamburgh-Cochin ♂.

In 1903, 12 pullets bred in Experiment 6 were mated with a cockerel bred in the same experiment. Eggs from this pen produced 119 chicks, with the following characters:—

COMB.—DR ROSE (*single*) ♀ × DR ROSE (*single*) ♂ gave 89 rose combs and 30 singles, or 2·9 D : 1 R. These were respectively indistinguishable from the pure rose and single combs (cf. Experiment 6).

DOWN.—DR BLACK (*buff*) ♀ × DR BLACK (*buff*) ♂ gave 88 blacks and 31 buffs, or 2·8 D : 1 R. Of these, 17 were black with whitish throats, 71 black, variably marked and shaded with brown, 9 dark buff, 5 buff ticked with black, 11 light buff, and 6 creamy white. Those that were reared developed their first plumage as follows: the blacks with whitish throats became clear black, the blacks marked with brown matured into a medley of nondescript blacks and browns, the variable buffs and creamy whites developed into buffs of various shades, some being more or less mis-marked with brown and black (cf. Experiment 6).

FEET.—RR 4 ♀ × RR 4 ♂ gave 119 with no e.t., or all R. Of these, 24 had malformed feet of various kinds, *e.g.*, two toes, united at the base, and bearing a single nail, otherwise they were quite healthy and vigorous (cf. Experiment 6).

SHANKS.—DR FEATHERED (*clear*) ♀ × DR FEATHERED (*clear*) ♂ gave 115 feathered and 4 clear; of these, approximately, 17 were fully feathered as in the Cochin grandparent, 20 three-fourths, 57 one-half, as in the parents, 13 one-fourth, 8 with feather traces on upper part of shanks, and 4 were quite clear and free from feathers (cf. Experiment 6).

FIRST CROSSES BRED WITH THEIR PARENTS (F_2).

The two following experiments give the results of breeding back the first crosses with one of the parents. The Mendelian expectation for the mating DR × DD is all dominants: for DR × RR it is equality of dominants and recessives, and for RR × RR it is, of course, all recessives.

Experiment 9.—Leghorn-Houdan ♀ × Leghorn ♂.

In 1903, five pullets bred in Experiment 1 were mated with a White Leghorn cockerel; eggs from this pen produced 135 chicks, with the following characters:—

COMB.—DR LEAF (*single*) ♀ × RR Single ♂ gave 74 leafs and 61 singles, or 1·2 D : 1 R. Of these, 8 were full leafs, 66 split leafs, 60 ordinary

singles, and 1 single with the hinder end somewhat thickened (cf. Experiments 1 and 7).

DOWN.—DR WHITE (*black*) ♀ × DD WHITE ♂ gave 135 whites, or all D. Of these, 66 were clear white and 69 white ticked with black (cf. Experiments 1 and 7).

FEET.—DR 5 (4) ♀ × RR 4 ♂ gave 63 e.t. and 72 with no e.t., or 1 D : 1.1 R. Of these, 56 had e.t. on both feet, 4 had e.t. on one foot only, 2 had long hallux on both feet, 1 had six toes on one foot, and no e.t. on the other, and 72 had no trace of e.t. (cf. Experiments 1 and 7).

SHANKS.—RR clear ♀ × RR clear ♂ gave 135 clear, or all R (cf. Experiments 1 and 7).

Experiment 10.—Hamburgh-Cochin ♀ × Hamburgh ♂.

In 1903, 12 pullets bred in Experiment 6 were mated with a Black Hamburgh cock; eggs from this pen produced 56 chicks, with the following characters:—

COMB.—DR ROSE (*single*) ♀ × DD Rose ♂ gave 56 rose combs, or all D. These were indistinguishable from the pure rose comb (cf. Experiments 6 and 8).

DOWN.—DR BLACK (*buff*) ♀ × DD Black ♂ gave 56 blacks, or all D. Of these, 34 were black with whitish throats, while 22 were slightly marked with brown, chiefly about the head (cf. Experiments 6 and 8).

FEET.—RR 4 ♀ × RR 4 ♂ gave 56 with no e.t., or all R. All were normal (cf. Experiments 6 and 8).

SHANKS.—DR FEATHERED (*clear*) ♀ × RR clear ♂ gave 35 feathered and 21 clear, or 1.6 D : 1 R. Of these, approximately, 19 were one-half feathered as in the DR parents, 6 were one-fourth, 10 had feather traces on the upper part of the shanks, and 21 were clear and quite free from feathers as in the R parent (cf. Experiments 6 and 8).

So far the experiments have been confined to the same kinds of matings used by Mendel and his successors, viz.: first crosses bred together (AB × AB) and first crosses bred with the parent breed (AB × A). The three following experiments are, however, rather more complicated, as in some instances three differential characters are concerned rather than the usual Mendelian pair, the matings being AB × C, AB × D, and AB × CD. In these cases it is difficult to apply the Mendelian terminology of D and R without some confusion, because some of the D's are themselves R to other D's, and some of the R's are themselves D over other R's. The omission of the Mendelian

terminology in these cases may serve a useful purpose in showing that the Mendelian principles of segregation are independent of the secondary question of dominance. The three following experiments were deliberately designed to put the Mendelian principles to a severe test, and as the sequel shows, the results (though necessarily complicated) so far as segregation is concerned, agree closely with the Mendelian expectation.

FIRST CROSS BRED WITH A DISTINCT PURE BREED (F_2).

Experiment 11.—*Leghorn-Houdan* ♀ × *Black Hamburg* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a Black Hamburg cock; eggs from this pen produced 101 chicks, with the following characters:—

COMB.—LEAF (*single*) ♀ × Rose ♂ gave 101 rose combs, or all. Of these, 58 were indistinguishable from the pure rose comb (cf. Experiment 2), and 43 were irregular rose combs with a double peak (cf. Experiment 4).

DOWN.—WHITE (*black*) ♀ × Black ♂ gave 52 whites and 49 blacks, or 1·0 : 1. Of these, 7 were clear white, 45 white ticked with black (cf. Experiment 2), 24 black with whitish throats, and 25 black with white heads (cf. Experiment 4).

FEET.—5 (4) ♀ × 4 ♂ gave 23 with e.t., and 78 with no e.t., or 1 : 3·3. Of these 10 had e.t. on both feet, 13 had e.t. on one foot only (cf. Experiment 4), and 78 had no trace of e.t. (cf. Experiment 2).

SHANKS.—Clear ♀ × clear ♂ gave 101 clear, or all, with no trace of feathers (cf. Experiments 2 and 4, 1 and 7).

Experiment 12.—*Leghorn-Houdan* ♀ × *Buff Cochin* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a Buff Cochin cockerel; eggs from this pen produced 106 chicks, with the following characters:—

COMB.—LEAF (*single*) ♀ × Single ♂ gave 60 leafs and 46 singles, or 1·3 : 1. Of these, 5 were full leafs, 55 split leafs (cf. Experiment 5), and 46 ordinary singles (cf. Experiment 3).

DOWN.—WHITE (*black*) ♀ × Buff ♂ gave 52 whites and 54 blacks, or 1 : 1·0. Of these, 6 were clear white, 46 white patched with buff and brown, and some with odd black ticks also (cf. Experiment 3), 54 were black variably marked and shaded with brown, and some with white ticks also (cf. Experiment 5).

FEET.—5 (4) ♀ × 4 ♂ gave 45 with e.t., and 61 with no e.t., or 1 : 1·3.

Of these 43 had e.t. on both feet, 2 had e.t. on one foot only (cf. Experiment 5), and 61 had no trace of e.t. (cf. Experiment 3).

SHANKS.—Clear ♀ × Feathered ♂ gave 106 feathered, or all. Of these, approximately, there were 68 half-feathered, 15 three-fourths, and 23 fully feathered (cf. Experiments 3 and 5).

FIRST CROSS BRED WITH A DISTINCT FIRST CROSS (F_2).

Experiment 13.—*Leghorn-Houdan* ♀ × *Hamburg-Cochin* ♂.

In 1903, 12 pullets bred in Experiment 1 were mated with a cockerel bred in Experiment 6; eggs from this pen produced 307 chicks, with the following characters:—

COMB.—LEAF (*single*) ♀ × ROSE (*single*) ♂ gave 139 rose combs, 77 leafs, and 91 singles. Of these, 83 were regular rose (cf. Experiment 2), and 56 were irregular rose combs with double peaks (cf. Experiment 4); 6 were full leafs, and 71 were split leafs (cf. Experiment 5); all the singles were normal (cf. Experiment 3).

DOWN.—WHITE (*black*) ♀ × BLACK (*buff*) ♂ gave 148 whites and 159 blacks, or 1:1.1. Of these, 20 were clear white, 87 white ticked with black (cf. Experiment 2), 41 white patched with buff and brown (cf. Experiment 3), 19 black with whitish throats, 32 black with white heads (cf. Experiment 4), and 108 black, variably marked and shaded brown, and some also ticked with white (cf. Experiment 5).

FEET.—5 (4) ♀ × 4 ♂ gave 127 with e.t. and 180 with no e.t., or 1:1.4. Of these, 108 had e.t. on both feet, 19 had e.t. on one foot only (cf. Experiments 4 and 5), and 180 had no trace of e.t. (cf. Experiments 2 and 3).

SHANKS.—Clear ♀ × FEATHERED (*clear*) ♂ gave 195 feathered and 112 clear, or 1.7:1. Of these, approximately, 92 were one-half feathered, as in the male parent, 31 one-fourth, 72 had feather traces on the upper part of the shanks (cf. Experiments 3 and 5), and 112 were clear with no trace of feathers (cf. Experiments 2 and 4).

COMBINATION OF TWO OR THREE PAIRS OF CHARACTERS IN F_2 .

So far we have dealt simply with the results of mating pairs of single characters separately, and now we have to consider how the Mendelian ratios work out when two or three pairs of single characters are taken together in individual birds. The following tables give, in black figures the Mendelian calculation of the numbers of each type expected, and in plain figures the actual numbers of each type observed in the various experiments of F_2 .

The following abbreviations are used to denote the types:—
wh. = white, bl. = black, bf. = buff downs; l.c. = leaf, s.c. = single,
r.c. = rose combs; e.t. = extra toe, no e.t. = no extra toe on feet.

(a) Combination of Two Characters.

EXPERIMENT 7.

Down and Comb.			Down and Feet.		
Mendelian calc.	Nos. obs.	Types	Mendelian calc.	Nos. obs.	Types
127·1	125	wh., l.c.	127·1	138	wh., e.t.
42·3	47	wh., s.c.	42·3	41	bl., e.t.
42·3	40	bl., l.c.	42·3	34	wh., no e.t.
14·1	14	bl., s.c.	14·1	13	bl., no e.t.
<hr/> 225·8	<hr/> 226		<hr/> 225·8	<hr/> 226	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types
127·1	135	l.c., e.t.
42·3	44	s.c., e.t.
42·3	30	l.c., no e.t.
14·1	17	s.c., no e.t.
<hr/> 225·8	<hr/> 226	

EXPERIMENT 8.

Down and Comb.		
Mendelian calc.	Nos. obs.	Types
66·9	62	bl., r.c.
22·3	26	bl., s.c.
22·3	27	bf., r.c.
7·4	4	bf., s.c.
<hr/> 118·9	<hr/> 119	

EXPERIMENT 9.

Comb and Feet.		
Mendelian calc.	Nos. obs.	Types
33·7	39	l.c., e.t.
33·7	35	l.c., no e.t.
33·7	24	s.c., e.t.
33·7	37	s.c., no e.t.
<hr/> 134·8	<hr/> 135	

EXPERIMENT 12.

Down and Comb.			Down and Feet.		
Mendelian calc.	Nos. obs.	Types	Mendelian calc.	Nos. obs.	Types
26·5	35	wh., l.c.	26·5	22	wh., e.t.
26·5	17	wh., s.c.	26·5	30	wh., no e.t.
26·5	25	bl., l.c.	26·5	23	bl., e.t.
26·5	29	bl., s.c.	26·5	31	bl., no e.t.
<hr/> 106·0	<hr/> 106		<hr/> 106·0	<hr/> 106	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types
26.5	27	l.c., e.t.
26.5	33	l.c., no e.t.
26.5	18	s.c., e.t.
26.5	28	s.c., no e.t.
<hr/> 106.0	<hr/> 106	

EXPERIMENT 13.

Down and Comb.

Mendelian calc.	Nos. obs.	Types
76.7	63	wh., r.c.
76.7	76	bl., r.c.
38.3	48	wh., s.c.
38.3	43	bl., s.c.
38.3	37	wh., l.c.
38.3	40	bl., l.c.
<hr/> 306.6	<hr/> 307	

Down and Feet.

Mendelian calc.	Nos. obs.	Types
76.7	62	wh., e.t.
76.7	86	wh., no e.t.
76.7	65	bl., e.t.
76.7	94	bl., no e.t.
<hr/> 306.8	<hr/> 307	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types
76.7	52	r.c., e.t.
76.7	87	r.c., no e.t.
38.3	41	s.c., e.t.
38.3	50	s.c., no e.t.
38.3	34	l.c., e.t.
38.3	43	l.c., no e.t.
<hr/> 306.6	<hr/> 307	

(b) Combination of Three Characters.

EXPERIMENT 7.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types
95.3	104	wh., l.c., e.t.
31.7	34	wh., s.c., e.t.
31.7	31	bl., l.c., e.t.
31.7	21	wh., l.c., no e.t.
10.5	13	wh., s.c., no e.t.
10.5	10	bl., s.c., e.t.
10.5	9	bl., l.c., no e.t.
3.5	4	bl., s.c., no e.t.
<hr/> 225.4	<hr/> 226	

EXPERIMENT 12.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types
13.2	11	wh., s.c., no e.t.
13.2	6	wh., s.c., e.t.
13.2	19	wh., l.c., no e.t.
13.2	16	wh., l.c., e.t.
13.2	17	bl., s.c., no e.t.
13.2	12	bl., s.c., e.t.
13.2	14	bl., l.c., no e.t.
13.2	11	bl., l.c., e.t.
<hr/> 105.6	<hr/> 106	

EXPERIMENT 13.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types
38.3	25	wh., r.c., e.t.
38.3	38	wh., r.c., no e.t.
38.3	27	bl., r.c., e.t.
38.3	49	bl., r.c., no e.t.
19.1	22	wh., s.c., e.t.
19.1	26	wh., s.c., no e.t.
19.1	19	bl., s.c., e.t.
19.1	24	bl., s.c., no e.t.
19.1	15	wh., l.c., e.t.
19.1	22	wh., l.c., no e.t.
19.1	19	bl., l.c., e.t.
19.1	21	bl., l.c., no e.t.
306.0	307	

From the above tables it will be seen that the various experiments give all the possible combination types, and that the actual numbers of these types are, on the whole, in fair agreement with the Mendelian expectation, calculated by means of the Mendelian ratios. Cases of slight deficiency or excess of certain types will, in most cases, be found to correspond with similar irregularities in the single characters. This leads to the important fact that each single character is inherited independently of the other, the combinations taking place apparently in accordance with the calculus of chance, as Mendel found in Peas. The above experiments with poultry thus confirm Bateson's previous experiments¹, and show clearly that there is no correlation between the down, comb, and foot characters observed, but that each is a "unit character" with an independent inheritance.

SUMMARY OF RESULTS (F_1 and F_2).

In summarising the results of the above experiments, the most natural method will be to deal first with each character separately, *i.e.*, (1) Comb; (2) Down; (3) Feet, etc., tabulating all the results under each, in the four Mendelian expectations, viz.: (a) all D's, (b) all R's, (c) 3 D : 1 R, (d) 1 D : 1 R. The details will be briefly reviewed under each character, afterwards the grand totals of all the characters will be also tabulated in the four Mendelian expectations.

The somewhat complicated Experiments 11, 12, and 13 will be brought into line with the others by regarding their results as D's and R's simply, irrespective of their complicated matings.

¹ Bateson and Saunders, Report I (1902), p. 110.

(1) Combs.

(a) All D's.

Gen.	Expt.	D	R
F ₁	1	105	0
F ₁	2	57	0
F ₁	4	6	0
F ₁	5	5	0
F ₁	6	107	0
F ₂	10	56	0
F ₂	11	101	0
Total observations ...		437	0
Mendelian calc.....		437	0

(b) All R's.

Gen.	Expt.	D	R
F ₁	3	0	60
Total observations ...		0	60
Mendelian calc.....		0	60

(c) 3 D : 1 R.

Gen.	Expt.	D	R	Ratio
F ₂	7	165	61	2·7 : 1
F ₂	8	89	30	2·9 : 1
F ₂	13	216	91	2·3 : 1
Total obs.		470	182	2·5 : 1
Mendelian calc....		489	163	3 : 1

(d) 1 D : 1 R.

Gen.	Expt.	D	R	Ratio
F ₂	9	74	61	1·2 : 1
F ₂	12	60	46	1·3 : 1
Total obs.		134	107	1·2 : 1
Mendelian calc....		120·5	120·5	1 : 1

In F₁, the Houdan leaf comb is dominant over both the Leghorn and Cochin singles (Experiments 1 and 5), in a few cases this dominance is complete and the full leaf is reproduced, while, in the majority, it is incomplete, consisting of all kinds of intermediate split leaves.

In F₁, the Hamburg rose comb is dominant over both the Leghorn and Cochin singles (Experiments 2 and 6), and in all cases the dominance is complete, the hybrid combs being indistinguishable from the pure rose comb.

In F₁ the Hamburg rose comb is also dominant over the Houdan leaf comb (Experiment 4), and in this we have a case of one dominant being recessive to another dominant. The dominance of rose over leaf is not so complete as that of rose over single, though more complete than that of leaf over single. No exceptions to dominance in F₁, in regard to combs, were observed in any of the experiments¹.

In F₂, the hybrid dominant leafs of F₁, mated together, gave dominant leafs and recessive singles in the proportion of 2·7 : 1 (Experiment 7); mated with pure recessive singles they gave dominant leafs and recessive singles in the proportion of 1·2 : 1 (Experiments 9 and 12), and mated with dominant rose they gave all dominant rose combs (Experiment 11).

¹ Cf. Bateson and Saunders, Report I (1902), pp. 94, 97, 98.

In F_2 , the hybrid dominant rose combs of F_1 , mated together, gave dominant rose and recessive singles in the proportion of 2·9 : 1 (Experiment 8), and mated with pure dominant rose they gave all dominant rose combs (Experiment 10).

(2) *Downs.*

(a) All D's.				(b) All R's.			
Gen.	Expt.	D	R	Gen.	Expt.	D	R
F_1	1	94	11	F_1	4	0	6
F_1	2	49	8	Total observations		0	6
F_1	3	53	7	Mendelian calc.		0	6
F_1	5	5	0				
F_1	6	107	0				
F_2	9	135	0				
F_2	10	56	0				
Total observations ...		499	26				
Mendelian calc. ...		525	0				

(c) 3 D : 1 R.					(d) 1 D : 1 R.				
Gen.	Expt.	D	R	Ratio	Gen.	Expt.	D	R	Ratio
F_2	7	171	55	3·1 : 1	F_2	11	52	49	1·0 : 1
F_2	8	88	31	2·8 : 1	F_2	12	52	54	1 : 1·0
					F_2	13	148	159	1 : 1·0
Total obs.		259	86	3·0 : 1	Total obs.		252	262	1 : 1·0
Mendelian calc.		258·7	86·2	3 : 1	Mendelian calc.		257	257	1 : 1

In F_2 , the hybrid dominant leafs of F_1 , mated with the hybrid dominant rose combs of F_1 gave dominant rose and leaf combs and recessive single combs in the proportion of 2·3 : 1 (Experiment 13).

Although the nature of the dominants and recessives raised in F_2 has not yet been tested in F_3 , yet judging by the structural details of the incomplete dominants and the recessives of F_2 there can be little doubt that the segregation is on Mendelian lines.

In F_1 the white plumage of the Leghorn is dominant over both the Houdan and Hamburg black (Experiments 1 and 2) and also over the Cochin buff (Experiment 3). In a few cases this dominance is complete and the clear white is reproduced, while in the majority it is incomplete, the white ground colour being ticked with black (Experiments 1 and 2) or patched with buff and brown (Experiment 3); the black ticking is slight and inextensive compared with the ground colour and the buff and brown patching is chiefly confined to the head, neck, and breast¹. A few apparent exceptions to dominance of white occurred in these matings,

¹ Cf. Bateson and Saunders, Report I (1902), pp. 95, 98.

including blacks, cuckoos, and buffs, but as the sequel shows, caution is necessary before we ascribe these exceptions to failure of dominance.

In F_1 the black plumage, both of the Houdan and the Hamburg, is dominant over the buff of the Cochin (Experiments 5 and 6), but in all cases the dominance is incomplete, the black ground colour being strongly marked and shaded with brown. The dominance of black is more complete in the down than in the adult plumage.

In F_2 the hybrid dominant whites of F_1 mated together gave dominant whites and recessive blacks in the proportion of 3:1:1 (Experiment 7), mated with a pure recessive black they gave dominant whites and recessive blacks in the proportion of 1:0:1 (Experiment 11), mated with a pure dominant white they gave all dominant whites (Experiment 9), and mated with a pure buff they gave whites and blacks in the proportion of 1:1:0 (Experiment 12).

In F_2 the hybrid dominant blacks of F_1 mated together gave dominant blacks and recessive buffs in the proportion of 2:8:1 (Experiment 8), and mated with a pure dominant black gave all dominant blacks (Experiment 10).

In F_2 the hybrid dominant whites of F_1 mated with a hybrid dominant black of F_1 gave whites and blacks in the proportion of 1:1:0 (Experiment 13). Although the nature of the dominants and recessives raised in F_2 has not yet been tested in F_3 , yet judging by the detailed down markings of the incomplete dominants of white and black parentage, there is little doubt that with these the segregation is on Mendelian lines, at the same time it must be pointed out that wherever the buff element is concerned in the parentage the variation is much more continuous than in F_1 (cf. Experiments 8, 12 and 13). It may be that white and black are elementary characters, and buff a compound one which in F_2 more than in F_1 is resolved into its component parts, or it may be that black and buff when once united in F_1 do not segregate so sharply as white and black undoubtedly do. In either case it may be significant that in F_1 the dominance of both white and black over buff is much less complete than that of white over black. Experiments are now in progress to test this question.

With regard to the few apparent recessives that occurred in the white matings of F_1 , I have only been able to follow up those of Experiment 1, and they have proved an interesting study. These 11 chicks were out of supposed pure white Leghorn hens by a pure recessive black Houdan cockerel (ticked with white), all were born with black down notwithstanding that their 94 birth-mates were dominant whites. These black chicks, though apparently similar in the down,

developed into two distinct types in their first plumage, 6 were black and 5 were cuckoo; of the 6 blacks, 5 were practically clear black save for a few inconspicuous white ticks in the crest, these exactly resembled in their plumage the Crève-Cœur breed, the remaining black was mottled all over with white, like a typical light Houdan (this unfortunately died); the 5 cuckoos were grey-white barred with blue-black, with odd black or white feathers; both the blacks and the cuckoos were shaded with brown as in the Houdan parent. Curiously, and unfortunately in some respects, the 6 blacks were all pullets and the 5 cuckoos all cockerels¹.

With regard to the black birds, the question naturally arose whether they were pure recessives RR or whether the usual dominant white character had receded, leaving them RD. In order to test this, the 5 black pullets were mated with a pure recessive black Houdan cockerel (mottled with white) (Experiment 15); eggs from this pen produced 48 chicks, all of which were black with white heads like the typical Houdan. These results show that the black pullets raised in Experiment 1 were in composition RR, for if they had been RD some dominant white chicks would surely have appeared in this experiment, when they were mated with a pure recessive.

[Note added December, 1904.

After this account was written one of the original white hens used in Experiments 1, 2 and 3 was found to have developed distinct colour-ticks in the hackles. To the impurity thus manifesting itself, the appearance of pure recessives in F_1 should, doubtless, be attributed.]¹

With regard to the nature of the exceptional cuckoo cockerels in Experiment 1, the experiments are not yet completed, though, so far, they have proved interesting, and bid fair to yield useful results. One of the cuckoo cockerels was mated with 2 of the black pullets; eggs from this pen produced 43 chicks, all of which had black down; 34 were ticked with white, 7 had white heads, and 2 were strongly shaded grey. All were more or less shaded with brown as in the Houdan; 31 of these were reared, and in their first plumage were 17 cuckoos and 14 blacks. Of the cuckoos 7 were cockerels and 10 were pullets, and of the blacks 8 were cockerels and 6 were pullets, so that the correlation of black with ♀ and cuckoo with ♂ in F_1 was not maintained in F_2 ¹.

¹ Later experiments demonstrate clearly that these exceptional black pullets and cuckoo cockerels are cases of sex-linked inheritance, the White Leghorn dam carrying the barred factor which (linked with maleness in her Z chromosome) was handed on to her (cuckoo) sons and not to her (black) daughters. (Note added 1924.)

The cuckoos were precisely similar to those of F_1 , having a grey-white ground barred with blue-black, with odd black or white feathers. All had a distinct brown shade in the plumage. The blacks were of two types, dark Houdans and Crèves, suggesting that the cuckoo male parent was giving off black gametes. No dominant whites appeared in this mating, suggesting that the cuckoo male parent was *not* giving off dominant white gametes.

Further experiments are now in progress to carry this Mendelian analysis of the cuckoo cock a stage further, although an interesting complication has recently arisen in the fact that this bird has in his second plumage moulted out almost *clear white*, a single feather only, on the back, being slightly tipped with grey. (See footnote p. 232.)

(3) Feet.

(a) All D's.				(b) All R's.			
Gen.	Expt.	D	R	Gen.	Expt.	D	R
F_1	1	103	2	F_1	2	0	57
F_1	4	6	0	F_1	3	0	60
F_1	5	4	1	F_1	6	0	107
				F_2	8	0	119
Total observations ...		113	3	F_2	10	0	56
Mendelian calc.		116	0	Total observations ...		0	399
				Mendelian calc.		0	399

(c) 3 D : 1 R.					(d) 1 D : 1 R.				
Gen.	Expt.	D	R	Ratio	Gen.	Expt.	D	R	Ratio
F_2	7	179	47	3·8 : 1	F_2	9	63	72	1 : 1·1
					F_2	11	23	78	1 : 3·3
Total obs.		179	47	3·8 : 1	F_2	12	45	61	1 : 1·3
Mendelian calc.		169·5	56·5	3 : 1	F_2	13	127	180	1 : 1·4
					Total obs.		258	391	1 : 1·5
					Mendelian calc.		324·5	324·5	1 : 1

In F_1 the extra-toe of the Houdan is dominant over the normal foot of the Leghorn, Hamburgh, and Cochin (Experiments 1, 4 and 5). In some cases the dominance is complete, the extra-toe being reproduced in its entirety; in other cases the dominance is incomplete, all stages of extra-toe being produced from the almost perfect toe down to the mere duplication of the nail; in a few cases the e.t. (in all its stages) is found on one foot only, the other foot being apparently normal; in a few cases there is simply an elongated hallux¹. A few apparent exceptions to dominance of e.t. occurred in Experiments 1 and 5.

¹ Cf. Bateson and Saunders, Report I (1902), p. 97.

In F_2 the hybrid dominant e.t.'s of F_1 mated together gave dominant e.t.'s and apparently recessive no e.t.'s in the proportion of 3·8 : 1 (Experiment 7); mated with pure recessive no e.t.'s they gave dominant e.t.'s and apparently recessive no e.t.'s in the varying proportions of 1 : 1·1 (Experiment 9), 1 : 1·3 (Experiment 12), 1 : 1·4 (Experiment 13), and 1 : 3·3 (Experiment 11).

The two exceptions to dominance in Experiment 1 of F_1 were fortunately of two sexes, and when mated together gave 22 chicks, of which 14 had e.t. and 8 with normal feet. The same cockerel was also mated with 4 Hamburgh-Cochin hens raised in Experiment 6, all, of course, with pure R normal feet, 24 chicks were raised, of which 11 had e.t. and 13 no e.t. The same pullet (Experiment 1) also gave some chicks with e.t. when mated with a pure Leghorn cockerel with R normal feet. These results prove that the apparently recessive feet with no trace of e.t. in Experiment 1 are in reality RD's, as both birds gave chicks with e.t. when bred together and with pure recessives. This is apparently a case where the usual dominant character has receded in F_1 to re-appear in F_2 , and may safely be described as a true instance of the failure of dominance¹. The fact of a recessive character, like normal foot, dominating occasionally in F_1 and proving in F_2 to be in reality RD is unfortunate, because it may lead to serious complications, *e.g.*, in Experiments 7, 9, 11, 12 and 13, noted above, we have no certainty that all the apparent recessives are RR's, as a few of them may be RD's, and if each bird with normal foot has to be tested individually in F_3 before it can be counted in F_2 , it will be impossible to test the foot character on a statistical basis without great labour and expense, and it is quite possible that on account of this complication the foot character will have to be abandoned in future experiments, notwithstanding that in reality its inheritance may be in accordance with the Mendelian principles. Judging broadly from the above experiments in F_2 , it is evident that the segregation is on Mendelian lines, the only notable exception being Experiment 11 where the ratio is 1 : 3·3 instead of the equality expected.

In this experiment, there is not only a large excess of recessives, but even the dominants are abnormal, tending towards the recessive character, for the majority of those with e.t. have it on one foot only, which is quite different from the normal result in all the other experiments, where the one-sided e.t.'s are in a small minority. These facts point to some abnormal disturbance in this experiment.

¹ Cf. Bateson and Saunders, Report I (1902), pp. 102, 113, 115.

(4) *Shank-feathering.*

(a) All D's.					(b) All R's.				
Gen.	Expt.	D	R		Gen.	Expt.	D	R	
F ₁	3	60	0		F ₁	1	2	103	
F ₁	5	5	0		F ₁	2	0	57	
F ₁	6	107	0		F ₁	4	0	6	
F ₂	12	106	0		F ₂	7	7	219	
Total observations ...		278	0		F ₂	9	0	135	
Mendelian calc.....		278	0		F ₂	11	0	101	
					Total observations		9	621	
					Mendelian calc.		0	630	
(c) 3 D : 1 R.					(d) 1 D : 1 R.				
Gen.	Expt.	D	R	Ratio	Gen.	Expt.	D	R	Ratio
F ₂	8	115	4	28·7 : 1	F ₂	10	35	21	1·6 : 1
Total obs.		115	4	28·7 : 1	F ₂	13	195	112	1·7 : 1
Mendelian calc....		89·2	29·7	3 : 1	Total obs.		230	133	1·7 : 1
					Mendelian calc....		181·5	181·5	1 : 1

In F₁ the shank-feathering of the Cochin is dominant over the clear shanks of the Leghorn, Houdan, and Hamburgh (Experiments 3, 5 and 6). In all cases the dominance is incomplete, the length and number of the feathers being reduced to a fairly uniform one-half. No exceptions to this incomplete dominance were observed.

In F₂, the hybrid dominant feathered shanks of F₁, mated together, gave a large number of dominant feathered shanks, with a few recessive clear shanks (Experiment 8); mated with pure recessive clear shanks, they gave dominants and recessives in the proportion of 1·6 : 1 (Experiment 10) and 1·7 : 1 (Experiment 13). The Mendelian expectation for Experiment 8 was 3 D : 1 R, while the actual result was most exceptional, being, in fact, nearer 30 : 1 than 3 : 1.

The nature of the dominants, too, was different, for, while the Mendelian expectation was approximately 30 full-feathered and 60 half-feathered, the actual result was 17 full-feathered, 20 three-fourths, 57 half-feathered, 13 one-fourth, and 8 with feather traces. In fact, the dominants in F₂ represented a continuous series of feathering, ranging from full to clear, while in F₁ they were uniformly half-feathered. In Experiments 10 and 13 there was also continuous variation among the dominants, but the series only extended from one-half-feathered to clear, and the number of recessives was not far from the Mendelian expectation. From this it would appear that the

Mendelian principles are at work in these aberrant phenomena, but are masked by something not yet perceived. It will be best, therefore, to reserve any attempt at explanation of them until the Mendelian analysis is completed in F_3 .

Both in F_1 and F_2 , among the recessive matings, a few slight traces of dominant feathering appear; these are apparently confined to Experiments 1 and 7, and, as similar traces appeared in the Houdan P_1 , it is evident that the impurity came from that side, especially as it was never observed in the Leghorn.

One curious feature in this impure inheritance, is that in both experiments, where it showed itself, the actual parents did not show it, and, in the case of Experiment 7, neither the two parents nor the grandparents showed it, though the collaterals did ("uncles") (cf. Experiments 1 and 7). The impurity, therefore, seems to have remained latent for two generations in the direct line, though appearing in the collaterals.

Grand Totals (F_1 and F_2).

(a) All D's.				(b) All R's.			
Characters	D	R		Characters	D	R	
Combs	437	0		Combs	0	60	
Downs	499	26 ¹		Downs	0	6	
Feet	113	3		Feet	0	399	
Shanks	278	0		Shanks	9	621	
Total obs.	1327	29 ¹		Total obs.	9	1086	
Mendelian calc. ...	1356	0		Mendelian calc. ...	0	1095	
(c) 3 D : 1 R.				(d) 1 D : 1 R.			
Characters	D	R	Ratio	Characters	D	R	Ratio
Combs	470	182	2.5 : 1	Combs	134	107	1.2 : 1.0
Downs	259	86	3.0 : 1	Downs	252	262	1.0 : 1.0
Feet	179	47	3.8 : 1	Feet	258	391	1.0 : 1.5
Shanks	115	4	28.7 : 1	Shanks	230	133	1.7 : 1.0
Total obs.	1023	319	3.2 : 1	Total obs.	874	893	1.0 : 1.0
Mendelian calc. 1006.5	335.5	3 : 1		Mendelian calc. 883.5	883.5	1 : 1	

The adding together of the results of different characters in different experiments may not be strictly legitimate, but, as each character in each experiment has been first dealt with separately, and all the details which go to make up the totals have been given, the objections to this method are reduced to a minimum, and are far outweighed by the advantages of the large numbers thus made available.

¹ See note of 1904, p. 232, which eliminates 26 of these exceptions. (Note added 1924.)

In regarding the 5560 observations as a whole, one cannot but be impressed by the close approximation to the Mendelian expectation; at the same time, it must not be forgotten that, although most of the characters have appeared to segregate, in accordance with the Mendelian principles, we do not yet know that the extracted recessives are pure, nor do we know that the complete dominants consist of pure and impure in the Mendelian proportions; several generations will have to be bred before these questions can be definitely determined.

If, however, the experiments be taken as they stand, the close agreement with the Mendelian expectation cannot be without significance.

Summary of Conclusions from Experiments with Poultry.

(1) When certain pure breeds are mated with their own kind, certain structural and colour characters breed true to type; in some of these characters there is little or no variation, while in others the variation about the type is considerable.

(2) When these pure breeds are crossed with one another, certain of these characters are usually dominant over the corresponding character, which is recessive. Dominant characters are rose comb, white plumage, extra toe, feathered shanks, white and blue shanks, crested head, brown egg-colour and broodiness, while leaf and single comb, black and buff plumage, normal foot, clear shanks, yellow shanks, uncrested head, white egg-colour and non-broodiness are all recessive to the above corresponding dominants. In their turn, some of these recessives are themselves dominant over others, *e.g.*, leaf comb and black plumage are dominant over single comb and buff plumage, which remain recessive.

Dominance appears to be of two kinds, *Complete* and *Incomplete*. Complete dominants are practically indistinguishable from the pure dominants; incomplete dominants are variable, showing the influence of the recessive character in different degrees, the intensity of the dominant character being correspondingly diminished. In some character matings the dominance is apparently always complete, in some it is always incomplete, and in others it is sometimes complete, but more often incomplete. On the whole, the incomplete dominants appear to be about twice as numerous as the complete dominants. The pure recessive is always quite distinct from both kinds of dominants.

(3) When the offspring of the dominant first crosses are bred together, and with various dominants and recessives, some of their

progeny exhibit the dominant, and others the recessive, character, the proportions of each being, as a rule, in close agreement with Mendel's law. In these crosses the dominants are again complete and incomplete, the former being indistinguishable from the pure dominants, and the latter corresponding to the incomplete dominants in the first crosses with fair consistency. The recessives are, as a rule, similar to the original ones, but their purity has not yet been tested.

(4) No correlation was found between the comb, down, and foot characters, each, apparently, being a unit-character with an independent inheritance. When any two or three of these characters were considered together in individual birds, the numbers of each type in the second crosses approximated closely to the numbers calculated by means of Mendel's law.

(5) A few exceptions to the general results stated in (2) and (3) may be briefly noted: (a) a few recessives appeared in some of the first crosses instead of the usual dominants; these proved to be of two kinds, impure and pure, the former giving some dominants when mated with a pure recessive (p. 234), while the latter did not (p. 232). The appearance of a few impure recessives in the first cross indicates that the normally recessive character (normal foot) may sometimes dominate, which fact may lead to future complications. The pure colour recessives in F_1 are, without doubt, to be ascribed to impurity in a white parent, signs of which subsequently revealed themselves. (b) In all the second crosses, where buff plumage and shank-feathering were concerned, the variation of the offspring appeared to be much more continuous than in the corresponding matings of the first crosses. Experiments are in progress to test the nature of these exceptions by Mendelian analysis¹.

¹ As these extensive and expensive experiments with Poultry were carried out without any financial assistance, it was unfortunately found impossible to continue them beyond the second generation. (*Note added 1924.*)

ON THE INHERITANCE OF COAT COLOUR IN HORSES¹

Recent experiments by the writer have demonstrated the Mendelian inheritance of coat colour in rabbits². These results suggested that the inheritance of coat colour in horses might also be in accordance with the Mendelian principles. In the case of horses, however, the ordinary method of direct experiment was impracticable, so that recourse was had to the valuable series of records contained in Weatherby's *General Stud Book of Race Horses*. This work consists of 20 volumes, containing fairly complete records of the age, colour, sex, and parentage of British thoroughbreds from the earliest accounts down to the end of 1904.

In the modern volumes, at all events, these records have been carefully registered, and with the allowance of a small margin of error may be safely accepted as scientific evidence, as the results of this paper show.

Professor Karl Pearson has already made use of this material in his memoir "On the Inheritance of Coat Colour in Horses³," but his statistical methods did not disclose any intrinsic differences in the heredity of the several colour-types. More recently, referring to the inheritance of eye and coat colour, Professor Pearson remarks that: "Before we leave the cases above it is just worth reiterating that nothing corresponding to Mendel's principles appears in these characters for horses, dogs, and men."

In regard to thoroughbred horses, he adds: "It is the same with every coat colour taken, its relative constancy depends largely on the extent to which it has appeared in the ancestry, and one by one black, bay, chestnut, grey must be dismissed by the Mendelian as neither 'recessive' nor 'dominant,' but as marking 'permanent and incorrigible mongrels⁴.'"

¹ Communicated to the Royal Society by Professor W. Bateson, F.R.S., Nov. 4, 1905. Read Dec. 7th, 1905, and reprinted from *Proc. Roy. Soc. B.* LXXVII. pp. 388-394 (1906).

² *Journ. Linn. Soc. (Zool.)*, XXIX. pp. 283-324 (1905). (See p. 166.)

³ *Phil. Trans. A*, CXCv. pp. 79-150 (1900).

⁴ *Biometrika*, II. pp. 214, 215 (1903).

A careful examination of the *Stud Book* records so far fails to give any support to Professor Pearson's statement: on the contrary, the records show clearly, for instance, that bay and brown are Mendelian dominants to chestnut which is recessive¹. For example, the bay and brown sires *St Simon*, *St Serf*, *Galopin*, *Ladas*, *Merry Hampton*, and *Cabin Boy*, mated with numerous chestnut mares, gave 370 foals, all of which were bays or browns. The following table gives the individual numbers:

TABLE I (DD × RR).

Pure Dominant Bay and Brown Sires, mated with Recessive Chestnut Mares.

Sires	Bay and brown foals	Chestnut foals	Total
<i>St Simon</i>	96	0	96
<i>St Serf</i>	83	0	83
<i>Galopin</i>	62	0	62
<i>Ladas</i>	56	0	56
<i>Merry Hampton</i>	44	0	44
<i>Cabin Boy</i>	29	0	29
Totals.....	370	0	370

The above numbers not only show the Mendelian dominance of bay and brown over chestnut, but they also prove that the individual sires concerned are homozygous bays and browns giving off no chestnut gametes.

It may be noted that all these sires had bay or brown parents and grandparents except *St Serf*, which had a chestnut grandparent.

Further records show that other bay and brown sires are heterozygous, giving off chestnut gametes on the average in equal numbers, in accordance with the Mendelian expectation.

For instance, the bay and brown sires *Royal Hampton*, *Donovan*, *St Angelo*, *Isinglass*, *Orvieto*, *Ayrshire*, *Florizel II*, *Pioneer*, *Isonomy*, *Melton*, *Wisdom*, and *Rose Window*, mated with numerous chestnut mares, gave 702 foals, of which 355 were bays and browns and 347 were chestnuts. These numbers are close to the Mendelian expectation of equality.

¹ In the recent volumes, about 95 per cent. of the colours registered are bay, brown, or chestnut, the small remainder consisting of black, grey, roan, and other colours.

The following table gives the individual numbers:

TABLE II (DR × RR).

Impure Dominant Bay and Brown Sires, containing Chestnut, mated with Recessive Chestnut Mares.

Sires	Bay and brown foals	Chestnut foals	Total
Royal Hampton	44	44	88
Donovan	47	33	80
St Angelo	37	41	78
Isinglass	28	34	62
Orvieto	32	30	62
Ayrshire	31	29	60
Florizel II	34	25	59
Pioneer	26	26	52
Isonomy	25	24	49
Melton	20	23	43
Wisdom	18	23	41
Rose Window	13	15	28
Totals.....	355	347	702

Of the above heterozygous bay and brown sires containing chestnut, *Royal Hampton*, *St Angelo*, *Isinglass*, *Orvieto*, *Isonomy*, *Melton*, and *Wisdom* had each a chestnut parent; *Donovan*, *Pioneer*, and *Rose Window* had both parents bay or brown, with a chestnut grandparent; *Ayrshire* had all the parents and grandparents bay or brown, with a chestnut great-grandparent; while *Florizel II* had all the parents, grandparents and great-grandparents bay or brown, with a chestnut great-great-grandparent. It will be noted that, notwithstanding these differences in ancestry, all are heterozygous, giving off chestnut gametes in about equal numbers, in accordance with the Mendelian expectation.

Further records show that the recessive chestnuts, variously extracted from bays and browns, as a rule breed true when mated together without reversion to their bay and brown ancestors, in accordance with the Mendelian conception of gametic purity.

For example, 100 chestnut sires, variously extracted, mated with about 600 chestnut mares of various extractions, gave 1104 foals, of which 1095 are recorded as chestnuts and 9 as bays or browns. That is to say, more than 99 per cent. of foals bred from chestnut parents are recorded as chestnuts, while less than 1 per cent. are recorded as exceptions to the rule. The apparent exceptions to the rule of chest-

nuts breeding true might have some significance if they were more numerous, but they are too inconsiderable to be of any certain value, and may simply represent breeders' or printers' errors.

In a work of such a magnitude and character as the *General Stud Book*, it is satisfactory to find that in a given case, tested by Mendel's law, 1 per cent. covers the margin of error, and the result reflects great credit on all those concerned in the compilation of the records.

The following table gives the individual numbers of 30 of the chestnut sires :

TABLE III (RR × RR).
*Chestnut Sires, of Various Extractions, Mated with Chestnut
Mares of Various Extractions.*

Sires	Bay and brown foals	Chestnut foals	Total
Amphion	0	56	56
Kendal	1	49	50
Wiseman	1	48	49
Chittabob	0	45	45
Despair	0	45	45
Juggler	1	41	42
Otterburn	1	40	41
Bend Or	0	40	40
Ocean Wave	1	38	39
Deuce of Clubs	0	36	36
Orion	0	35	35
Sainfoin	0	28	28
Southampton	1	27	28
Esterling	0	27	27
Necromancer	0	27	27
Satiety	0	25	25
Saraband	0	24	24
Llanthony	1	23	24
Hagioscope	0	21	21
Timothy	0	19	19
Hazlebatch	0	18	18
Lowland Chief	0	18	18
Lord Lorne	0	17	17
Aperse	0	16	16
Albert Victor	0	16	16
Dan Dancer	0	16	16
Gold	0	15	15
Peter	0	13	13
Friar's Balsam	0	13	13
Young Woodpecker	0	11	11
Monte Cristo	0	11	11
Seventy other chestnut sires...	2	237	239
Totals,	9	1095	1104

It being established that chestnut is a Mendelian recessive, the question arises, What is the critical feature which distinguishes chestnut from bay and brown? An examination of many horses leaves little doubt that the chestnut is distinguished by the absence of black "points" (mane, tail, and legs) always present in bay and brown. In all these types the colour of the coat presents a considerable range of tint. The differentiating pair of Mendelian characters is thus apparently the presence or absence of black pigment in the "points."

Summary.

In modern thoroughbred horses chestnut colour is a Mendelian recessive to bay and brown, which are dominant characters.

The consideration of other colours being excluded, bays and browns are of two kinds: (a) Those that when mated with chestnuts will give *no* chestnut offspring. (b) Those that when mated with chestnuts will give, on an average, half their offspring chestnuts and the remainder bays or browns. Similarly, the recessive chestnuts, variously extracted from the dominant bays and browns, breed true, as a rule, when mated together, without reversion to their bay or brown ancestors. To this rule, 9 exceptions were found in 1104 cases, and it is not impossible that these may be due to errors in the records.

Note added January 31, 1906.

In the paper read on January 18, Professor Weldon disputes these conclusions, while admitting that, contrary to Professor Pearson's statement, chestnuts breed true within a very small percentage of error. Since my paper was read, a fresh tabulation has been made of a sample including more than 2500 offspring recorded from chestnut mares, taken without selection.

Omitting greys, two sires of doubtful identity and sires with less than 10 foals each, it appears that

30 RR sires	give	455 R + 3D,
25 DD	„	450 D + 4R,
54 DR	„	496 D + 507 R.

This evidence, with that previously collected and with Professor Weldon's fresh evidence, points to about 1 per cent. of exceptions in the records of both the chestnuts and the pure dominants. Professor Weldon's argument is based entirely on the alleged existence of exceptions. The Stud Book is remarkably accurate, but there is a sufficient

margin of demonstrable error in the returns to make it possible that the few exceptions which cannot be eliminated are due rather to mistake than to any physiological peculiarity in the animals concerned. As a matter of fact, a sensible proportion of the original records are afterwards corrected, either in the Stud Book itself or in the Racing Calendar. In illustration of this, it may be mentioned that *Ben Battle*, a sire recorded in the Stud Book as chestnut, appears in the Racing Calendar several times as bay or brown, and Mr G. H. Verrall, who has kindly given help in this matter, writes that it is practically certain that *Ben Battle* never ran as a chestnut.

Several alleged chestnuts, ascribed to *Hackler*, *Wolf's Crag*, and other pure dominant sires can be similarly corrected. Among the residual exceptions are some which were born dead or died unnamed. Very few indeed can be proved to have appeared in public uncorrected. Other errors probably arise through an incorrect return of the sire's name. For instance, a certain sire appears to give a total of 43 dominants and three chestnuts from chestnut mares; a scrutiny revealed that two of these chestnuts (which happen to be among the four mentioned above) were from one chestnut mare. Moreover, the same mare is credited with a *bay* foal by a *chestnut* sire. These three exceptions occur in four consecutive returns from one stud. Considering the extreme rarity of any exception, the coincidence seems to point to inaccuracy in the returns of the breeder in question. In Professor Weldon's tabulation such a sire would be ranked as a DR, and the 43 bays and browns he gave would go to create the excess of dominants which Professor Weldon found to result from the mating $RR \times DR$ —an excess obviously due to the inclusion of such cases in that category. It is, of course, not impossible that genuine exceptions do occur. They must, however, be exceedingly rare in any case, and I am disposed to doubt whether the returns made to the Stud Book have the extreme precision which would be required to establish such occurrences.

Finally, it would appear that the distinct properties of chestnuts must be ascribed to segregation rather than to ancestry, seeing that their behaviour in heredity is entirely different from that of bays and browns, though their ancestral composition may for several generations have been the same.

This analysis was undertaken without any knowledge of previous work on similar lines, but several papers stating more or less concordant conclusions have since been discovered. The memoir by Crampe¹,

¹ *Landw. J. B.*, 1888, xvii., especially p. 828.

mentioned by Professor Weldon in the discussion on his paper of January 18, gives, as I now find, extensive tables drawn from German sources, showing that within a small margin of error chestnut (*fuchs*) breeds true. Of the exceptions, several, as he shows, are probably mistakes, and the rest he regards as dubious. Wilckens¹, as the result of a similar analysis on a large scale, found 24 recorded exceptions to the purity of "*fuchs*" per 1000 matings. The absolute purity of chestnuts, however bred, is asserted by Mr Wilfrid Scawen Blunt² for the Kehailan strain of Arabs. The same assertion is also made for the horses called "*rote*" (?red chestnut) in the Jutland breed by Jensen³. Finally, we have a general statement by Hayes⁴, applicable to all kinds of horses, that in the vast majority of cases a foal from a chestnut dam by a chestnut sire is of a chestnut colour.

The existence of the two kinds of dominants, and the conclusions based thereon have not, so far as I know, been previously recognised.

¹ *Landw. J. B.*, 1888, xvii. p. 575.

² *The Nineteenth Century and After*, 1906, January, p. 68.

³ *Deut. Pferdezucht*, i. Hft. 11, 1904. (Original not seen; abstract in *J. B. Landw. Pfl. u. Tierzüchtung*, 1905, ii. p. 273.)

⁴ *Points of the Horse* (3rd ed.), 1904, p. 326.

XVI

MENDEL'S LAW OF HEREDITY¹

Mendel experimented with seven pairs of pure bred "characters" in peas, viz. yellow and green seeds (cotyledons), round and wrinkled seeds, purple and white flowers, tall and dwarf stems, inflated and constricted pods, green and yellow pods, axial and terminal flowers. In each pair, when crossed, Mendel found the first-named character dominant over the other, which he called recessive: *e.g.* yellow crossed with green gave seeds all with yellow cotyledons. In this case yellow is dominant over green, which is recessive.

Mendelian dominance has recently been found to hold good in a large number of characters in many species of plants and animals; *e.g.* in my own experiments I have found the following among many others (the dominant character is named first):

Peas: Round and wrinkled seeds; yellow and green cotyledons.

Sweet Peas: Tall and dwarf stems (Cupid); long and round pollen grains.

Primula: Palm and fern leaf; thrum and pin-eyed.

Antirrhinum: Red and white flowers; white and yellow flowers.

Tomato: Red and yellow flesh; yellow and white skin of fruit.

Orchids: Spotted and striped flowers.

Poultry: Rose and single comb; white and black plumage.

Rabbits: Coloured and white coat; short and angora coat.

Horses: Bay and chestnut colour; brown and chestnut colour.

Recent experiments show that the phenomenon of complete dominance is by no means universal. In many cases the dominance is incomplete, distinct traces of the recessive character being visible in the crossbreds, *e.g.* in my poultry experiments white \times black plumage gave both clear white and white ticked with black, the dominance of white being incomplete in the latter case. In some cases hybrid characters appear to be intermediate between the parents, *e.g.* some characters in orchid hybrids.

¹ Read by request before the Scientific Committee of the Royal Horticultural Society on March 20th, 1906, and reprinted from *Journ. Roy. Hort. Soc.* xxxii. pp. 227-229 (1906).

In a few cases the hybrid characters are like neither parent, but appear to revert to an ancestral form, *e.g.* "Black Knight" sweet pea \times "Pink Cupid" gave all wild purple crossbreds. In a few cases, again, the hybrid characters are like neither parent, nor are they reversions, but give an apparently new character, *e.g.* the blue Andalusian fowl is a distinct hybrid breed between a black and a splashed white, and never breeds true. In nearly all the cases, however, so far as they have yet been investigated, Mendel's law of segregation and purity is evident. It is, moreover, evident that many of the so-called intermediate hybrids are really due to the association of two distinct dominant characters each with an independent Mendelian heredity.

MENDEL'S LAW OF SEGREGATION AND PURITY.

In the second generation, when the hybrid dominants were self-fertilised, Mendel found that segregation or splitting of the characters took place in the ratio of three dominants (D) to one recessive (R); *e.g.* the hybrid yellow peas, self-fertilised, gave on the average 75 per cent. yellows and 25 per cent. greens, both types often appearing in the same pod. The law of segregation was also confirmed in the above experiments with various plants and animals; the recessive character, after "skipping a generation," re-appeared apparently unchanged.

In the third generation Mendel found that the extracted recessives bred true, without reversion to their dominant parents or ancestors; *e.g.* the green peas extracted from the hybrid yellows bred true greens, with no trace of yellow. Mendel also tested the dominants of the second generation and found them to be of two kinds—in the ratio of one pure to two hybrid.

The pure dominants bred true, while the hybrid dominants segregated again into 3D : 1R; *e.g.* the yellows bred from the hybrid yellows were one-third pure yellows which bred true with no trace of green, and two-thirds hybrid yellows, which gave 75 per cent. yellows and 25 per cent. greens.

Mendel continued these experiments through several generations with the same result. The Mendelian formula for segregation is therefore 1DD : 2DR : 1RR, *i.e.* 25 per cent. pure dominants, 50 per cent. hybrid dominants, and 25 per cent. pure recessives.

The law of purity was also confirmed in the above experiments with various plants and animals, the extracted recessives in all cases breeding true, with no trace of the dominant parents and ancestors.

THE MENDELIAN THEORY.

Mendel did not apparently offer any explanation of the facts of dominance, nor has any satisfactory theory of dominance yet been propounded.

Mendel, however, brought forward a simple theory, which fully accounts for both the facts of segregation and purity, viz. the segregation of the gametes (germ-cells) of the hybrid, so that on the average one-half of the gametes carry the dominant character and one-half the recessive character. No gamete carries both.

This is known as the theory of gametic segregation or gametic purity. On this hypothesis the gametic constitution of the offspring of the hybrid dominants ($D \times R$) will be on the average ($DR \times DR = 1DD : 2DR : 1RR$) 25 per cent. pure dominants, 50 per cent. hybrid dominants, and 25 per cent. pure recessives. This result is in close agreement with the actual numbers Mendel obtained in his experiments.

PRACTICAL APPLICATION OF MENDEL'S LAW.

When the Mendelian characters coincide with the "points" desired by the breeder, as they do in many cases, a knowledge of Mendel's law will enable him to get what he wants in the shortest possible time. If the desired character is a recessive, it will breed true at sight.

If it is a dominant, several individuals may have to be bred from before the pure dominant is found; *but once found it will breed true*. When several Mendelian characters are desired in combination, a much larger number of individuals will be required to secure the pure form; but once found no "fixing" will be required; it breeds true at once. The old system of "fixing" by many years' selection leaves all to chance, and, in the light of present knowledge, is largely a waste of time.

When the desired "point" of the breeder is not a simple Mendelian character, but rather a compound one made up of more than the simple Mendelian unit, as is evident in certain cases, the breeder must rely on the assistance of the Mendelian experimenter, who will proceed to analyse it by exact methods. Once the Mendelian elements are discovered, the compound character will be as easily worked by the breeder as a simple one. The phenomenon of dominance apparently explains the oft-observed facts of characters "skipping a generation."

The facts of dominance show that the outward appearance of an individual is often no guide at all to its breeding potentialities, and that a knowledge of its gametic constitution is the only guide to its

heredity. This can only be secured by a Mendelian analysis. Recent experiments with mice, rabbits, sweet peas, and stocks show clearly, *e.g.*, that the gametic constitution of albinos (whites) is often very complex.

When more than one pair of Mendelian characters are concerned in the cross, the average result can be easily calculated, *e.g.* a hybrid round yellow pea will give:

$$(3R + 1W) \times (3Y + 1G) = 9RY + 3RG + 3WY + 1WG^1.$$

Mendel's law shows the necessity of breeding from single individuals, or, if more than one be bred from, care should be taken that each individual of the batch has the same gametic constitution.

The facts of correlation or coupling of characters should be carefully watched and noted by the breeder, or his calculations may be upset. Last, but not least, Mendelian experiments with plants and animals have shown clearly that, often, reciprocal crosses give similar results. These may serve a useful purpose in exposing once more the popular delusion that the "male parent gives the colour, while the female parent gives the form."

Many other questions of practical value are involved in Mendel's law of inheritance, but further experiments are necessary before one can venture to deal with them confidently.

¹ For full details of this case see p. 143.

XVII

MENDELIAN CHARACTERS IN PLANTS AND ANIMALS¹

Recent experiments with many kinds of plants and animals have largely extended the application of Mendel's law of heredity.

In my own experiments and observations, for instance, the Mendelian principles have been evident in such widely different organisms as peas and rabbits, sweet peas and horses, tomatoes and poultry, orchids and Man.

The main object of the experimenter has been to discover the Mendelian characters in each type of plant and animal by means of Mendel's methods.

In many cases this has been apparently easy, while in others it has been more difficult.

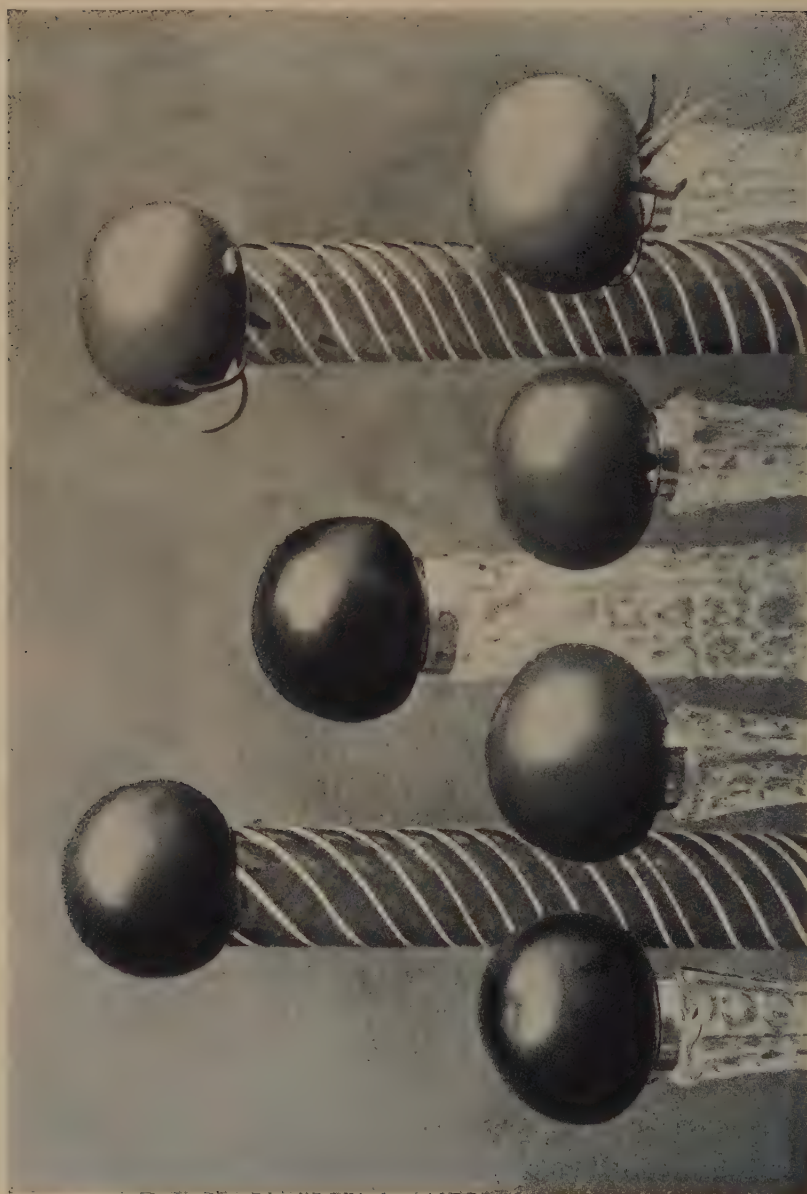
In Mendel's classical experiments with peas, the characters were patent, consisting simply of pairs of contrasts, *e.g.* round and wrinkled seeds, yellow and green cotyledons. Many similar cases have been found in other plants and in animals, and these usually follow the simple rules of dominance, segregation, and purity.

In these simple cases the outward or zygotic character of a pure plant or animal is presumably represented in the germ-cells or gametes by a single factor or determiner. In other cases, however, the zygotic character, though apparently simple, is really compound, being represented in the gametes by more than one factor.

Thus Mr Bateson, Miss Saunders and Mr Punnett have recently demonstrated that red flower-colour in sweet peas and stocks is due to the association of two gametic factors, purple colour to three factors, while hoariness in stocks has been shown by them to be due to no less than four distinct gametic factors.

These compound characters are not often to be detected at sight, and for the most part have to be subjected to a Mendelian analysis ere their true nature is discovered.

¹ Read at the Third International Conference on Genetics, London, July 31st, 1906 and reprinted from *Roy. Hort. Soc. Rep. Conf. Gen.* pp. 114-128, figs. 26-31 (1907).



F₂ 'Fireball'

F₂ Carmine

F₁ 'Fireball'

F₂ Gambo

'Golden Queen'
F₂ 'Golden Queen'

Fig. 95. Tomatoes.

Showing dominance of red over yellow flesh, and yellow over white skin in F₁ and segregation of these characters in F₂.

What could appear more simple, for instance, than such characters as the red colour of the fruits of the 'Fireball' tomato, the red colour of the flowers of the 'Crimson King' antirrhinum, the yellow-grey coat of the 'Belgian Hare' rabbit, or the rose comb of the 'Black Ham-burgh' fowl?

All these characters breed true to themselves, and have done so for many generations; yet, as my experiments show, all are really compound characters, each being represented in the gametes by more than one factor.

THE RED COLOUR OF THE 'FIREBALL' TOMATO.

The 'Fireball' tomato is a pure race, bearing red fruits: it has bred true to colour with me for at least ten generations. The shade of colour of the ripe fruits corresponds with that of 'Rouge Tomate' (tomato red) in *Répertoire de Couleurs*, t. lxxx. (tone 1): the peculiar fiery-red colour is due to the red flesh showing through a bright yellow skin.

In my experiments 'Fireball' was crossed with 'Golden Queen,' a race bearing yellow fruits. In F_1 all the cross-breeds were indistinguishable from 'Fireball,' red colour being dominant and yellow recessive (fig. 95). In F_2 segregation into three red to one yellow took place (42:13). In this generation, however, there were four distinct and discontinuous types, two reds, and two yellows. One type of red was like the original 'Fireball,' while the other was quite different, corresponding with 'Rouge Caroubier' (carmine red) in *Rép. de Coul.* t. cxiii. (tone 4); this shade is due to the red flesh showing through a white or colourless skin (fig. 95).

One type of yellow was quite different from the original 'Golden Queen,' corresponding with 'Jaune Gomme Gutte' (gamboge yellow) in *Rép. de Coul.* t. xxv. (tone 4); this shade is due to the yellow flesh showing through a bright yellow skin. The other type of yellow was like the original 'Golden Queen' corresponding with 'Jaune Soleil' (sunflower yellow) in *Rép. de Coul.* t. xxiii. (tone 3); this shade is due to the yellow flesh showing through a white skin (fig. 95).

These four types occurred in F_2 approximately in the ratio of 9:3:3:1 respectively (31:11:10:3), suggesting that the Mendelian characters in this case are two pairs, which are apparently (1) red and yellow flesh, red being dominant and yellow recessive; (2) yellow and white skin, yellow being dominant and white recessive. It is probable, however, that the unit-characters are really simply (1) presence (R) and absence (r) of red in the flesh; (2) presence (Y) and absence (y) of

yellow in the skin; presence being dominant and absence recessive in both.

In that case the gametic formula of 'Fireball' would be $(R + Y)$, 'Golden Queen' would be $(r + y)$, the carmine red would be $(R + y)$, and the gamboge yellow would be $(r + Y)$.

It is evident, therefore, that the red colour of the 'Fireball' tomato is due to at least two gametic factors.

Broadly speaking, red and yellow tomatoes may be said to behave as Mendelian characters, red being dominant and yellow recessive: at the same time Mendelian analysis shows that there are at least two types of red tomatoes, viz. red flesh in a yellow skin and red flesh in a white skin: similarly there are at least two types of yellow tomatoes, viz. yellow flesh in a yellow skin and yellow flesh in a white skin.

The practical importance of these results to the breeder lies in the fact that any of these four colour types can be quickly fixed (no matter how they may have arisen) by anyone possessing a knowledge of the Mendelian principles, and their various behaviours when crossed can be faithfully predicted for any number of generations.

THE RED COLOUR OF 'CRIMSON KING' ANTIRRHINUM.

The race of dwarf *Antirrhinum majus* grown in gardens as 'Crimson King' has red corolla segments corresponding with the shade 'Rouge Caroubier' (carmine red) of *Rép. de Coul.* t. cxiii. (tone 4).

In my experiments this form was crossed with 'Yellow Prince,' a dwarf race with yellow segments corresponding with the shade 'Jaune Soufre' (sulphur yellow) in *Rép. de Coul.* t. xviii. (tones 1 and 2).

All the F_1 cross-breds were indistinguishable from 'Crimson King,' red colour being dominant and yellow recessive. In F_2 segregation took place, there being approximately three 'Crimson King' to one 'Yellow Prince' (116 : 41).

Similarly 'Yellow Prince' crossed with 'White Queen,' a dwarf race with white segments, gave in F_1 cross-breds which were indistinguishable from 'White Queen,' white being dominant and yellow recessive. In F_2 segregation took place, there being approximately three 'White Queen' to one 'Yellow Prince' (37 : 13).

When, however, 'Crimson King' was crossed with 'White Queen,' all the cross-breds in F_1 were reds, but a different shade from that of 'Crimson King'; the shade of the cross-breds corresponded with 'Rouge

Amarante' (amaranth red) in *Rép. de Coul.* t. clxviii. (tones 3 and 4). In F_2 segregation into four types took place, there being approximately nine amaranth red, three 'Crimson King,' three 'White Queen,' one 'Yellow Prince' (81 : 22 : 26 : 8).

This result suggests that the red colour of 'Crimson King' is really a compound of red and yellow represented in the gametes by two distinct factors, R and Y, which, when associated, produce the zygotic red of 'Crimson King'; in the zygote the red colour predominates over the yellow, and so long as the two colours are associated 'Crimson King' breeds true to colour, but when dissociation takes place through crossing, the compound red yellow of 'Crimson King' is segregated into amaranth red and the sulphur yellow of 'Yellow Prince'.

In these three colour forms of antirrhinum, red, yellow, and white, the Mendelian character pairs are evidently not red and yellow, red and white, and yellow and white, as might be supposed, but are apparently two pairs only, viz. (1) presence (R) and absence (r) of red, presence being dominant and absence recessive; (2) presence (Y) and absence (y) of yellow, absence being dominant and presence recessive.

The genetic formula of 'Crimson King' may therefore be regarded as $(R + Y)$, amaranth red as $(R + y)$, 'Yellow Prince' as $(r + Y)$, and 'White Queen' as $(r + y)$. On this basis the whole of the results are clear, and the inheritance is strictly in accordance with the Mendelian principles.

One interesting and curious feature of these experiments with antirrhinum is the demonstration of recessiveness of presence of yellow sap and the apparent dominance of a negative quality.

As in the case of the tomatoes, the practical importance of these results to the breeder lies in the fact that any of the four colour types can be quickly fixed, no matter how they may have arisen, by anyone possessing a knowledge of the Mendelian principles, and their various behaviours when crossed can be faithfully predicted for any number of generations².

¹ Both the red and yellow colours concerned are apparently sap-colours, being soluble in water, and each solution gives a distinct chemical reaction. A suggestive demonstration of the compound nature of the red colour of 'Crimson King' may be seen when a solution of the amaranth red is added to a solution of 'Yellow Prince'; this gives a similar solution to that obtained from 'Crimson King,' and both solutions give the same chemical reactions.

² At the Conference Miss Wheldale suggested that 'White Queen' was not a white but a cream (cf. p. 317).

It is true that 'White Queen' is not an absolute albino, seeing that it has a yellow

GREY COAT COLOUR IN THE 'BELGIAN HARE' RABBIT.

In my experiments the pure-bred 'Belgian Hare' with a grey coat was crossed with the pure-bred 'White Angora' with a white coat. In F_1 all the offspring had grey coats (see fig. 93). In F_2 there were approximately nine grey : three black : four white (127 : 44 : 53) (see fig. 94.)

The colour ratio in F_2 suggests that at least two pairs of Mendelian factors are concerned which appear to be (1) presence (C) and absence (c) of colour, presence being dominant and absence recessive; (2) grey (G) and black (B) colour, grey being dominant and black recessive.

In that case the gametic formula of the 'Belgian Hare' would be (C+G), and that of the 'White Angora' (c+B); the new character 'black' which appeared in F_2 being thus introduced by the Albino Angora.

From this it would appear that the coloured coat of a rabbit is due to the meeting of two distinct gametic factors, one of which may determine the presence of the pigment, while the other determines the colour of that pigment. If, for instance, C be present, the animal will be coloured, if absent it will be white; if both C and G be present it will be coloured grey, while if C and B be present it will be coloured black.

These results with rabbits confirm Prof. Cuénot's experiments and conclusions with similar coat-colours in mice.

Since my results were published, Mr Bateson has suggested that in such cases the coat-colours may be due to at least three pairs of gametic factors, viz. (1) presence (C) and absence (c) of colour; (2) presence (G) and absence (g) of grey; (3) presence (B) and absence (b) of black; presence being dominant and absence recessive in each case. In that

palate and two rows of yellow hairs within the corolla tube, but the five corolla segments are pure white when mature, and no trace of the red or yellow sap-colours could be found when the white segments were tested chemically.

For the sake of simplicity the account of my results was confined to the white, yellow, and red corolla segments of the three races. With regard to the remainder of the flower, the yellow palate and the yellow hairs within the corolla tube are common to all the three races and evidently belong to an independent Mendelian character, all three forms being homozygous in that character.

With regard to the remainder of the corolla tube, this is white in 'White Queen' and 'Yellow Prince,' and amaranth red in 'Crimson King.' When 'Crimson King' was crossed with 'White Queen' and with 'Yellow Prince' all the cross-breds had red corolla tubes in F_1 , while in F_2 segregation into red tubes and white tubes took place *among the reds only*, all the whites and yellows having white tubes. Further experiments are necessary to determine the precise nature of these 'Delila' forms.

case the gametic formula of the 'Belgian Hare' would be $(C + G + B)$, and that of the 'White Angora' would be $(c + g + B)$, both being homozygous in B.

Either interpretation covers the known facts, and further experiments are necessary to determine which is correct. In any case, however, it is clear that the pure-breeding grey coat-colour of the 'Belgian Hare' is a compound character represented in the gametes by at least two distinct factors.

THE ROSE COMB OF THE 'BLACK HAMBURGH' FOWL.

In my experiments the pure-bred 'Black Hamburg' with a rose comb, crossed with the pure-bred Houdan with a leaf comb, gave in F_1 cross-breeds with modified rose combs. In F_2 there appeared a small proportion of true *single* combs (7 in 70). These results suggest that the homozygous rose and leaf combs are not simple Mendelian characters, but are probably compounds of rose on single, and leaf on single, respectively. In rose crossed with leaf combs, the two pairs of Mendelian factors may well be: (1) presence (R) and absence (r) of rose; (2) presence (L) and absence (l) of leaf; presence being dominant to absence in both cases, single (S) being common to both. In that case the gametic formula of rose comb may be regarded as $(R + l + S)$, and that of leaf comb as $(L + r + S)$.

These results confirm the similar experiments and conclusions of Messrs Bateson and Punnett with rose and *pea* combs.

It seems clear, therefore, that the pure-breeding rose comb of the 'Black Hamburg' fowl is a compound character represented in the gametes by at least two distinct factors.

THE NATURE OF MENDELIAN CHARACTERS.

The foregoing illustrations show some of the difficulties encountered by the experimenter in the determination of Mendelian characters in plants and animals. It is evident that the precise determination of unit-factors can only be secured by means of careful and exhaustive experiments.

When we find such apparently simple zygotic characters as those noted above giving a simple Mendelian result in certain crosses and yet in others proving to be gametically compound, the question naturally arises whether many other of the apparently simple Mendelian characters are not also compound in their gametic constitution.

Is it not possible, for instance, that some of the original Mendelian characters in peas may be due to more than one gametic factor?

For example, in cotyledon colour in peas, might not the character pairs be really presence and absence of yellow on a basis of green, rather than the contrasting yellow and green? Is it not possible that many of the so-called contrasting pairs of Mendelian characters are really compound, and that the true unit-characters are simply presence and absence?

REVIEW OF EXPERIMENTS.

In view of the possible reduction of Mendelian characters in plants and animals to the simple presence and absence of unit-characters, it may be useful to review briefly the Mendelian characters found in my own experiments.

PEAS.

In my experiments with peas, the Mendelian characters met with are the same as those discovered by Mendel, viz. yellow and green cotyledons, round and wrinkled seeds, tall and dwarf stems—the first-named of the pair being dominant over the other, which is recessive. As suggested above, the Mendelian contrasting pair, yellow and green, might be regarded as presence and absence of yellow on a basis of green. On this view, the characters yellow and green would belong to two distinct pairs, instead of one as Mendel supposed, and these would be presence (Y) and absence (y) of yellow, and presence (G) and absence (g) of green, presence being dominant over absence. The gametic formula of the pure-breeding yellow pea based on green would, on this view, be (Y+G), and the zygote yellow owing to dominance.

The gametic formula of the green pea would be (y+G) and the zygote green. It will be observed that both the yellow and the green peas are homozygous in G.

The wild pea has yellow cotyledons, and on the view that its yellow is based on green, the evolution of the green pea from the yellow might be explained by the mutational absence of the yellow factor in a certain gamete.

With regard to the pair of Mendelian contrasts, round and wrinkled seeds, the precise physiological nature of the irregular shrinking of wrinkled peas is hardly yet understood. Mr R. P. Gregory found that in round peas the starch grains were large and oval in shape, while in

wrinkled peas they were very small, rounded, and frequently compound¹. Professor de Vries apparently regards the wrinkling of peas as similar in nature to the wrinkling of the sugar maize, *i.e.* due to lack of starch. He states that "the sugar is only accumulated as a result of an incapacity of changing it into starch²." If this is so, then the Mendelian pair, round and wrinkled, might be regarded as presence and absence of roundness (starchiness) on a wrinkled basis (sugariness), presence being dominant over absence. Similarly, the Mendelian contrasting pair, tall and dwarf stems, might be regarded as presence and absence of tallness on a dwarf basis, presence being dominant over absence.

SWEET PEAS.

In my experiments with Sweet Peas, four pairs of Mendelian characters have, so far, been met with, *viz.* coloured and white flowers, purple and red flowers, tall and dwarf habit, long and round pollen grains—the first-named of the pair being dominant over the other, which is recessive.

With regard to the first two pairs, it has been clearly demonstrated by Mr Bateson, Miss Saunders, and Mr Punnett³ that three pairs of unit-factors are concerned in the sap colours of sweet pea flowers, *viz.* presence (C) and absence (c) of first colour factor (probably a colour-forming stuff), presence (R) and absence (r) of second colour factor (probably an enzyme), presence (B) and absence (b) of blueness.

A coloured flower depends on the simultaneous presence in the zygote of the two colour factors C and R. If both the factors are present, the flower will be red; if either C or R is absent, the flower will be white. If three factors C, R, and B are present, the flower will be purple; if B is absent, the flower will be red; if either C or R is absent, the flower will be white. From this it is evident that the two pairs of characters—coloured and white flowers, purple and red flowers, which in my experiments behaved as simple Mendelian pairs—are really due to three pairs of unit-factors, each pair being presence and absence of a certain unit, presence being dominant over absence.

With regard to the remaining characters met with in my experiments, tall and dwarf habit might be regarded as presence and absence of tallness on a dwarf basis, as in the peas, while long and round pollen

¹ *The New Phytologist*, II. (1903), p. 226.

² *Species and Varieties* (1904), pp. 283, 289.

³ Report III. *Evol. Com. Roy. Soc.* 1906.

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might be regarded as presence and absence of longness on a round basis, presence being dominant in both cases.

POPPIES.

In my experiments with *Papaver somniferum*, three pairs of Mendelian characters were met with, viz. coloured and white flowers, purple and red flowers, black and white basal area of petals—the first-named of the pair being dominant over the other, which is recessive. The first two pairs are probably, like the sweet pea, due to three pairs of unit-factors—presence and absence of C, presence and absence of R, presence and absence of B—presence being dominant. The remaining pair, black and white basal area of petals, may be regarded as presence and absence of black pigment, presence being dominant.

ANTIRRHINUMS.

In my experiments with *Antirrhinum majus*, as we have already seen, two pairs of Mendelian characters have been found, viz. white and yellow corolla segments, red and yellow corolla segments, the first of the pair being dominant over the other, which is recessive. The unit-factors in these two cases seem to be absence and presence of yellow sap, presence and absence of red sap, respectively, presence being recessive in the yellow, and dominant in the red (cf. p. 317).

TOMATOES.

In my experiments with tomatoes, as already seen, two pairs of Mendelian characters have been found, viz. red and yellow flesh, yellow and white skin, the first-named of the pair being dominant over the other, which is recessive. The unit-factors in these two cases seem to be presence and absence of red in the flesh, and presence and absence of yellow in the skin, respectively, presence being dominant in both cases (see fig. 95).

PRIMULAS.

In my experiments with *Primula*, three pairs of Mendelian characters were met with, viz. red and green stems, palm and fern leaves, thrum and pin eyes, the first-named of the pair being dominant over the other, which is recessive.

Red and green stems may be regarded as presence and absence of red on a green basis, presence being dominant and absence recessive.

The application of the presence and absence hypothesis to palm and fern leaves is not so obvious.

If we regard this as presence and absence of palm on a fern basis, we are at once met by the difficulty that the fern leaf appears to be an elongated palm leaf. If, on the other hand, we regard it as presence and absence of fern on a palm basis, this would imply dominance of fern over palm in the zygote, while experiments show, on the contrary, that palm leaf is dominant over fern leaf. Similarly with thrum and pin eye, if we regard it as presence and absence of thrum on a pin basis, we are met by the difficulty that pin eye or long style seems to be an elongated thrum or short style; while on the other hand, if we regard it as presence and absence of pin on a thrum basis, this would imply dominance of pin over thrum in the zygote, and experiments show, on the contrary, that thrum eye is dominant over pin eye.

ORCHIDS.

In my experiments and observations with orchid hybrids of various genera and species, three pairs of Mendelian characters have been found, viz. purple sap colour and albino, spotted sap and striped sap patterns (see fig. 91), white and green areas, the first-named of the pair being dominant over the other, which is recessive. The first pair may be regarded as presence and absence of purple sap, presence being dominant. The others may be regarded respectively as absence and presence of sap areas, and absence and presence of green plastids, presence being apparently recessive.

Many other characters in orchids, both pigmental and structural, are obviously Mendelian, but more evidence and much careful investigation are necessary before one can venture to deal confidently with such complicated material.

RABBITS.

In my experiments with rabbits, fourteen pairs of Mendelian characters have so far been found, which may be classified as follows, the first-named of the pair being dominant over the other, which is recessive:

(a) Coat colour, five pairs, viz. coloured and white (see figs. 93 and 94), grey and black, grey and yellow, black and yellow, full and dilute (full colours are grey, black, and yellow, and their respective dilutions blue-grey, blue, and blue-fawn).

(b) Coat patterns, eight pairs, viz. Himalayan white and clear white,

clear yellow and tortoise yellow, self-coloured and Himalayan white, English-marked and self-coloured, Tan-marked and self-coloured, Dutch-marked and self-coloured (the heterozygote of this is variably marked), English-marked and Dutch-marked, plain and silvered (fig. 96).

(c) Coat length and texture, one pair, viz. short and angora (see figs. 93 and 94).

With regard to the five Mendelian pairs of coat-colours, the first four might be regarded, as Mr Bateson suggests, as presence and absence of a specific colour, presence being dominant. The original grey might be regarded as based on black and yellow, black being absence of grey, and yellow being absence of black. The remaining pair, full and dilute, may be regarded as presence and absence of full on a dilute basis, presence being dominant.

With regard to the eight Mendelian pairs of coat patterns, all may be regarded as presence and absence of colour in certain areas, presence being dominant, except in the English and Tan patterns, where presence is apparently recessive.

With regard to the one pair of Mendelian characters for coat length and texture, short and angora, the application of the presence and absence hypothesis is not so obvious. If we regard this as presence and absence of short on an angora basis, we have the difficulty that the long coat of the angora appears to be a lengthened short coat. If, on the other hand, we regard it as presence and absence of angora on a short basis, this would imply dominance of angora over short in the zygote, while experiments show, on the contrary, that short coat is dominant over angora coat.

POULTRY.

In my experiments with poultry, eight pairs of Mendelian characters were met with, viz. rose and single comb, leaf and single comb, extra toe and normal foot, crested and plain head, feathered and clear shanks, white and yellow shanks, white and black plumage, white and buff plumage; the first-named of the pair being dominant over the other, which is recessive.

With regard to the combs, we have already seen that the unit-characters may be regarded as presence and absence of rose, presence and absence of leaf, presence being dominant, absence of either being single comb on which the rose and pea are presumably based. (It is possible also that the large single comb of the Mediterranean races is due to a separate unit-factor based on the original small single comb.)



Fig. 96. Coat Patterns in Rabbits.

English-marked	Self-coloured (G. 10)	Dark Dutch (G. 8)	Dutch-marked (G. 5)
Light Dutch (G. 2)	Himalayan	F ₁ Himalayan × Clear White	Clear White (G. 0)

(See also pp. 388 and 460.)

With regard to the foot characters, the dominance of extra toe over normal foot was found to be both incomplete and irregular, but segregation and gametic purity were evident, the unit-factors being apparently presence and absence of extra toe, presence being usually dominant.

With regard to shank feathering, dominance of feathered over clear shanks was found to be incomplete but regular, while segregation was irregular, but gametic purity evident, the unit-factors being apparently presence and absence of shank feathers.

The remaining pairs of Mendelian characters may be respectively regarded as presence and absence of crest, absence and presence of yellow pigment in the shanks, absence and presence of black pigment in the plumage, absence and presence of yellow pigment in the plumage. It will be noted that presence is dominant over absence in all cases except the black and yellow pigments, in which presence is apparently recessive though incompletely.

HORSES.

In my investigations in coat-colour in thoroughbred horses, I have found that chestnut colour is a Mendelian character, recessive to both bay and brown, which are dominant characters.

The unit-factors in this case are apparently presence and absence of black pigment in the points on a basis of red.

SUMMARY OF EXPERIMENTS.

From the brief survey given above, it will be seen that out of a total of 44 pairs of Mendelian characters met with in my experiments with plants and animals, no less than 41—or rather more than 93 per cent.—may be regarded as favourable to the hypothesis of presence and absence of unit-factors; the remaining three—or rather less than 7 per cent.—being more favourable to Mendel's original view of contrasting characters. Further experiments and the observations of others are necessary to determine the question, but in the meantime it may be interesting to inquire into the possible behaviour of these unit-factors in the processes of fertilisation and gameto-genesis.

THE BEHAVIOUR OF UNIT-FACTORS IN FERTILISATION.

In pure breeding, Mendel presumed that two like factors pair in the process of fertilisation—one factor from the male parent and one from the female parent—and when the resulting zygote produces gametes the two factors segregate, one factor going into one gamete and the other

into another. In cross-breeding, Mendel presumed that two unlike but contrasting factors pair in fertilisation, and when the resulting hybrid zygote produces gametes, the two contrasting factors segregate, one going into one gamete and the other into another: *e.g.* a pea with green cotyledons produces gametes carrying the factor G, and a pea with yellow cotyledons produces gametes carrying the factor Y. Then the green pea (G) self-fertilised, or fertilised with another green pea (G), produces a zygote (GG) which is green, and this produces gametes carrying G.

Similarly a yellow pea self-fertilised produces a yellow zygote (YY), which produces gametes carrying Y. When a green pea is cross-fertilised by a yellow pea, the hybrid yellow zygote is YG, and this produces two kinds of gametes, Y and G.

This is Mendel's view of the process—presuming as he did, that the unit-characters consist of pairs of contrasting characters. The hypothesis of presence and absence of unit-factors, however, necessitates a somewhat different view of the process.

On this view, a yellow pea is based on green, and produces gametes carrying two factors—one for yellowness (Y) and one for greenness (G). When self-fertilised, or fertilised with another yellow pea, the corresponding factors pair and the resulting zygote is yellow based on green (YY + GG). When the zygote produces gametes the corresponding factors segregate and each gamete has the constitution (Y + G).

Similarly a green pea produces gametes carrying two factors—one for greenness (G) and one for absence of yellowness (y). When self-fertilised, or fertilised with another green pea, the corresponding factors pair, and the resulting zygote is green with the constitution (yy + GG). When the zygote produces gametes the corresponding factors segregate, and each gamete has the constitution of (y + G).

So much for the process of pure breeding.

In cross-breeding the process would be as follows: A green pea, producing gametes (y + G), crossed with a yellow pea producing gametes (Y + G), would produce a hybrid yellow zygote of the constitution (Yy + GG). The hybrid zygote would produce two kinds of gametes (Y + G) and (y + G), one representing yellow based on green, and the other absence of yellow based on green. The practical result is, of course, the same on Mendel's view and on the hypothesis of presence and absence; it is the interpretation of the process that is fundamentally different.

THE NATURE OF THE 'ABSENCE' FACTOR.

Presuming that the presence and absence hypothesis is the correct interpretation, the question arises:

What is the nature of the presumed gametic factor for absence? A factor for presence is concrete and tangible, but a factor for absence is not so easily comprehended.

With regard to the possible nature of the 'absence' factor, three distinct views present themselves.

(1) There may be a concrete factor literally representing 'absence.'

(2) The factor for 'absence' may represent simply 'presence' in a dormant or latent state.

(3) There may be no factor at all, the presumed factor for 'absence' being simply nothing.

The first view is perhaps the simplest in the abstract, yet it is difficult to comprehend, and also to understand how such a negative factor could have originated.

The second view is, perhaps, the most plausible, but it is open to the serious objection that it implies that 'absence' is not real but only apparent; there is also the further objection that many cases are now known where the 'presence' factor itself exists in a dormant or latent state.

The third view is, perhaps, the most practical, inasmuch as 'absence' is not represented by anything, but this implies a non-pairing of factors in cross-breeding, and the question arises as to how segregation takes place in such cases. In pure breeding, segregation of the pair of factors for 'presence' would be normal, and in the case of two 'absences' neither pairing nor segregation would be necessary; the only difficulty therefore, is as to how segregation takes place in the gamete of a hybrid carrying some non-paired factors.

Such a process, however, is not inconceivable, for in most cases there would be both paired and unpaired factors together, and where segregation of the paired factors takes place it is conceivable that the same process might also segregate the unpaired factors, the 'presence' factor going into one gamete, nothing corresponding with it going into the other.

All three views are possible, and all are open to some objection; in the present state of knowledge it is difficult to say which of the three is the most reasonable. On the whole, the last view, that 'absence' is

simply nothing, certainly appeals to the practical mind, and is perhaps, of the three, the one least open to objection.

On this view mutational variations may consist simply of the addition of new unit-factors and the subtraction of old ones.

The evolution of races, of plants under cultivation and animals under domestication, has most certainly been made possible by these mutational variations.

The precise determination of the unit-factors in plants and animals —by Mendelian analysis or otherwise—is therefore of the utmost importance both to the biologist and the practical breeder.

The biological problem of the immediate future will be not so much the origin of species as the origin of unit-factors.

XVIII

MENDEL'S LAW OF HEREDITY AND ITS APPLICATION TO POULTRY BREEDING¹

Mendel was an Austrian monk, who afterwards became Abbot of Brünn. Born in 1822, he died in 1884. From 1855—1865 Mendel carried out his classical experiments with peas in the gardens of his cloister, and discovered the law of heredity, which will always be associated with his name. The paper announcing Mendel's discovery was published by the Brünn Natural History Society, but it remained practically unknown to the outside world for thirty-five years: it was not until 1900—sixteen years after Mendel's death—that the paper was found, and given to the world by Professor Hugo de Vries. Since then, though little more than seven years have passed away, Mendel's law has been critically tested by many experimenters in many lands, and has been found to apply to a large number of characters in various kinds of plants and animals, including man.

On the occasion of this conference it will, perhaps, be most fitting to confine ourselves to the consideration of those experiments which have been made with the domesticated fowl. A large number of Mendelian experiments with fowls have been carried out at Cambridge by Mr W. Bateson, F.R.S., the pioneer of Mendelism in this country. In this important work Mr Bateson has been ably assisted by Mr R. C. Punnett, while the experiments carried out by Dr C. B. Davenport, at the Carnegie Experiment Station in America, and by the writer, have also served to confirm the application of Mendel's law to poultry breeding. Time will not allow me to give details of these experiments, which are fully recorded in the Reports to the Evolution Committee of the Royal Society, 1902, 1905, and 1906, and in Publication No. 52 of the Carnegie Institution, Washington, 1906. Altogether, a number of structural and colour characters in poultry have been found to follow Mendel's law, and there is no doubt that many more yet remain to be discovered. (See p. 214.)

¹ Read at the Second National Poultry Conference, Reading, July 9th, 1907, and reprinted from *Rep. Nat. Poult. Conf.* Reading, pp. 89-96 (1907).

Mendelian Characters in Fowls. Mendelian characters consist of pairs of contrasts. In most cases one of the pair may be taken to represent the presence of a unit-character, while the other represents its absence. For instance, rose comb and single comb in fowls behave in heredity as a Mendelian pair of contrasting characters, rose comb representing presence of the unit-character roseness, and single comb its absence. Every poultry breeder knows the difference between a rose comb and a single comb, so that it is not necessary to describe these characters at this Conference. When a pure-bred rose-combed fowl, *e.g.*, a Black Hamburg, White Dorking, or Wyandotte, is crossed with a pure-bred, single-combed fowl, *e.g.*, a Leghorn, Minorca, or Cochin, no

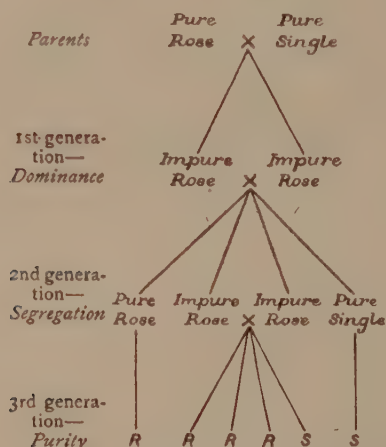


FIG. 97. GENERATIONS OF ROSE AND SINGLE COMBS.

matter which way the cross is made, we find that all the cross-breds have rose combs. In Mendelian terms, rose comb is dominant over single comb which is recessive. When the rose-combed cross-breds are bred together, we find that, on the average, three-fourths of the offspring have rose combs, while one-fourth have single combs. The recessive single comb, after skipping a generation, reappears in a quarter of the offspring. When these extracted single combs are bred together, they breed true to the single comb character, notwithstanding the fact that both their parents and one-half of their ancestors had rose combs. The rose-combed individuals of the second generation, when bred from in the third generation, are found to be of two kinds: on the average, one-third are pure rose combs, breeding true to the rose comb character, while

two-thirds are impure rose combs, throwing singles again, like their parents, the first crosses. The preceding diagram illustrates the results of crossing pure rose combs with pure single combs, and their behaviour in subsequent generations (fig. 97).

Mendel's Law of Segregation. Mendel's law is based on experimental facts like these, and in order to give a reasonable explanation of such facts, Mendel conceived the idea of the segregation of characters in the germ-cells. Mendel supposed, as Darwin did, and as we all do, that each heritable character is represented in the germ-cells (*i.e.*, the egg-cells of the hen and the sperm-cells of the cock) by a material factor or determiner. In the particular case we are considering the heritable character is rose comb, and single comb is regarded as absence of roseness. In pure breeding Hamburgs, for instance, the factor for roseness is presumably present in every germ-cell of both sexes, consequently all the Hamburg offspring have rose combs. Similarly, in pure breeding Leghorns the factor for roseness is presumably absent from every germ-cell of both sexes, consequently all the Leghorn offspring have single combs. In the cross-breeds of the rose-combed Hamburg and the single-combed Leghorn, according to Mendel's conception, when the germ-cells are formed segregation or splitting of characters takes place, with the result that the factor for roseness is present in one half of the germ-cells of both sexes, and absent in the other half. Consequently, when the cross-breeds breed together, on the average, one-fourth of the offspring will have pure rose combs, one-half impure rose combs, and one-fourth single combs. This is precisely the result obtained in our experiments, as we have already seen. The following diagram will illustrate the Mendelian conception of the segregation of factors in the germ-cells. The squares represent individual birds, and the circles their germ-cells. *R* represents the germinal factor for rose comb, and *S* its absence, or single comb (fig. 98).

As it is with the rose comb of the Hamburg, White Dorking and Wyandotte, so it is with the pea comb of the Indian Game and Brahma, the leaf comb of the Houdan, and the V comb of the Polish. All these behave as Mendelian characters, and are dominant over the original single comb. As it is with comb structures, so it is with the simple plumage colours. For instance, the pure white plumage of the White Leghorn and White Dorking is dominant over the black, red or yellow colours of the Black Hamburg, Black Minorca, Houdan, Indian Game, Brown Leghorn, and Buff Cochin. The dominant white cross-breeds bred together give on the average three whites to one coloured. The

extracted coloured birds bred together give all coloured offspring. In other words, pure white and coloured plumage behave as a Mendelian pair of contrasting characters. Curiously enough, it is only pure whites that dominate colour. Speckled whites, like the White Wyandotte, Silkie and White Rose-combed Bantam, and the splashed white of the Andalusian, are, on the contrary, recessive to colour, giving coloured cross-breds. With regard to the interesting phenomenon of dominance, it must be carefully noted that Mendel's law of segregation is altogether

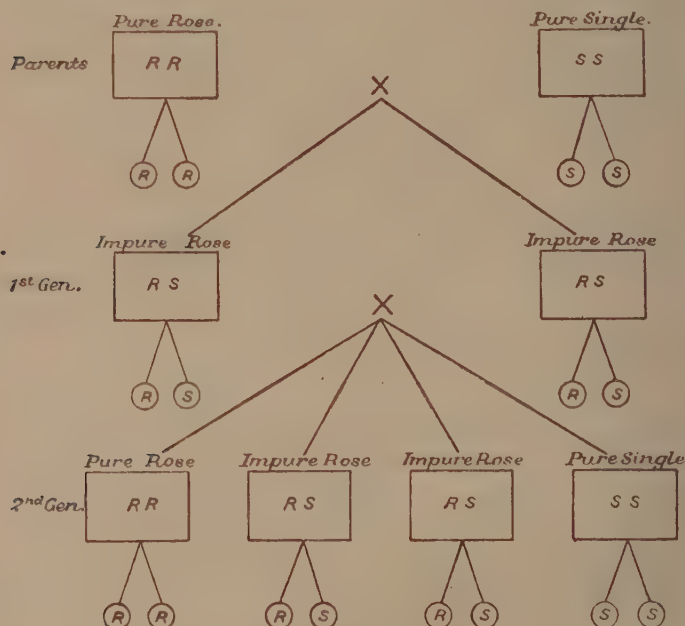


FIG. 98. MENDEL'S LAW OF SEGREGATION IN COMBS.

independent of the question of dominance. In poultry the dominance of one character over another is seldom absolute and complete. For instance, pure white crossed with colour gives white birds, but in most cases some coloured ticks are to be found scattered here and there on the white ground of the cross-breds. This absence of complete dominance does not affect Mendel's law, which is a law of segregation and not of dominance. The important point is that the pure white plumage, though modified by the cross with coloured plumage, comes out pure in the second generation.

The Case of the Andalusian Fowl. Perhaps the most interesting illustration of Mendelism in poultry is the case of the Andalusian fowl. For more than half a century breeders have been mating Blue Andalusians together, and yet to-day the blue colour is no more fixed than it was fifty years ago. If two winning blues with a "blue" pedigree be mated together, on the average only one-half of their offspring will be blues, while one-fourth will be blacks and one-fourth will be splashed whites.

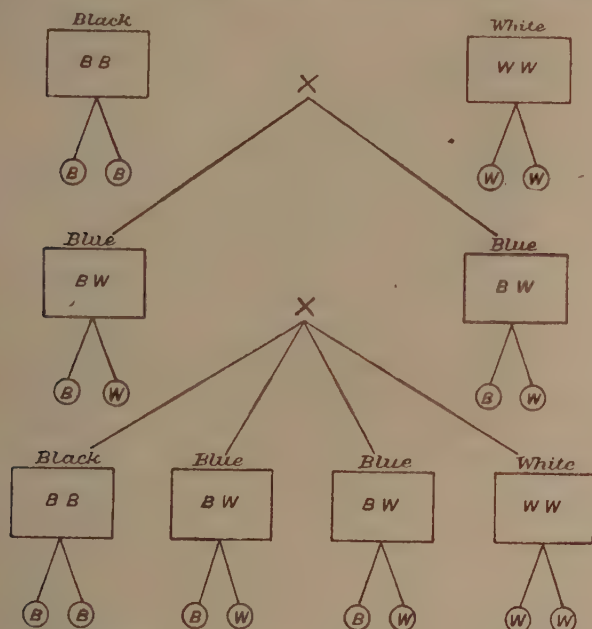


FIG. 99. MENDEL'S LAW APPLIED TO BLUE ANDALUSIAN FOWLS.

The fact is that the blue colour of the Andalusians is a Mendelian hybrid between black and splashed white, and so long as blue is bred with blue, so long will the three colours black, blue and white be thrown. If the blacks are bred together they give all blacks. If the splashed whites are bred together they give all splashed whites, while if the blacks are bred with the splashed whites they give all *blues*! If the blacks are bred with blues, they give equal numbers of blacks and blues. If the splashed whites are bred with blues they give equal numbers of splashed whites and blues. The only way to breed all blues is therefore to mate together the two off-colours black and splashed white, which to the

breeder may appear a paradoxical result. The Mendelian characters in this case are black and splashed white, and their combination gives the Blue Andalusian.

The preceding diagram illustrates the Mendelian nature of the Andalusian fowl. The squares represent individual birds and the circles their germ-cells. *B* represents the germinal factor for black, and *W* for splashed white (fig. 99).

Besides the various comb structures and simple plumage colours which have been shown to have a Mendelian inheritance, there are other structural and colour characters in fowls and bantams which, so far as experiments have gone, appear to be Mendelian. Such characters, for instance, as the crest, beard and muff of the Houdan and Polish, Silkie and Frizzled plumage, various colours of shanks, skin and plumage, and others. Of all the characters in poultry that have been worked with so far, only two appear to be doubtfully Mendelian, viz.: extra toe and feathered shanks, in these cases segregation takes place but is irregular, no doubt this is due to some complication not yet understood. (See p. 214.)

Practical Value of Mendel's Law. The practical value of Mendel's law is that once the Mendelian characters are ascertained, the breeder is able to calculate beforehand the results he will get in cross-breeding. Suppose, for instance, a breeder crosses the rose-combed Black Hamburg with the single-combed White Leghorn. The breeder knows that whichever way the cross is made he will get rose-combed white cross-breeds, because rose-comb and pure white plumage are Mendelian characters and dominant over single comb and black plumage. According to Mendel's law he knows further that by mating the rose-combed white cross-breeds together, he will get, on the average, three rose-combed to one single-combed, and three whites to one black, and that taking both pairs of characters together there will be, on the average, nine rose-combed whites, three rose-combed blacks, three single-combed whites, and one single-combed black. According to Mendel's law he knows further that all the single-combed blacks will breed true; that on the average one-third of the rose-combed blacks will breed true, while two-thirds of them will throw single-combed blacks; that, similarly, one-third of the single-combed whites will breed true, while two-thirds of them will throw single-combed blacks. Similarly, with the nine rose-combed whites, on the average, one will breed true, two will throw single-combed whites, two will throw rose-combed blacks, while the remaining four will throw both single-combed whites and single-combed blacks. In the same way the results of mating back the first crosses with each of the parent breeds

can be easily calculated by the breeder. Armed with this new knowledge the breeder can easily and quickly make new breeds by simple combinations of different Mendelian characters, at the same time avoiding the old and slow system of fixing a character by continued selection which leaves everything to chance. In conclusion, it is obvious that the practical value of Mendel's law to the poultry breeder depends wholly on the discovery of the Mendelian characters. Mendelian characters can only be discovered by precise and exhaustive experiments, and it is by carrying out these critical experiments that science can be of real service to the practical breeder. So far, in the discovery of Mendelian characters in poultry, science has only made a beginning. The point, however, lies in the fact that a beginning has been made, and that where formerly all was chaos and confusion, order has now appeared and a law of heredity has been discovered.

XIX

ON THE INHERITANCE OF EYE-COLOUR IN MAN¹

The following notes on the inheritance of Eye-colour in Man are based on material examined by the writer in the village of Burbage, Leicestershire. During the past three years, 139 pairs of parents and 683 of their offspring have been examined, with the following results :

Eye-colour in man depends almost wholly on the colour of the iris. The colour of the iris varies considerably in different families and often in different individuals of the same family. This variability is due partly to the presence or absence of different pigments on the anterior and posterior surfaces of the iris, and partly, in all probability, to actual differences in the structure of the iris.

In the Report of the Anthropometric Committee of the British Association for 1880, the following statement concerning the nature of eye-colour in man is given by Mr Charles Roberts (pp. 134 to 136) :

"The iris, on which the colour of the eye depends, is a thin membranous structure, composed of unstriped muscular fibres, nerves, and blood-vessels, held together by a delicate network of fibrous tissue. On the inner surface of this membrane there is a layer of dark purple pigment called the *uvea*...and in brown eyes there is an additional layer of yellow (and, perhaps, brown-red) pigment on its outer surface also, and in some instances there is a deposit of pigment amongst the fibrous structures. In the albino, where the pigment is entirely absent from both surfaces of the iris, the bright red blood is seen through the semi-transparent fibrous tissues of a *pink* colour; and in blue eyes, where the outer layer of pigment is wanting, the various shades are due to the dark inner layer of pigment—the *uvea*—showing through fibrous structures of different densities or degrees of opacity.

"The eyes of new-born infants...are dark blue, in consequence of the greater delicacy and transparency of the fibrous portion of the iris; and

¹ Communicated to the Royal Society by Professor W. Bateson, F.R.S., May 7th, 1907, read Nov. 14th, 1907 and reprinted from *Proc. Roy. Soc. B.* lxxx. pp. 85-96 (1908).

as these tissues become thickened by use, and by advancing age, the lighter shades of blue and, finally, grey are produced, the grey, indeed, being chiefly due to the colour of the fibrous tissues themselves. In grey eyes, moreover, we see the first appearance of the superficial layer of yellow pigment in the form of isolated patches situated around the margin of the pupil or in rays running across the iris.

"In the various shades of green eyes the yellow pigment is more uniformly diffused over the surface of the iris, and the green colour is due to the blending of the superficial yellow pigment with the blue and grey of the deeper structures. In the hazel and brown eyes the *uvea* and the fibrous tissues are hidden by increasing deposits of yellow and brown pigment on the anterior surface of the iris, and when this is very dense, black eyes are the result."

The above statement agrees well with my own observation, though I would add that the presence of the superficial layer of yellow pigment, when only slightly developed, is to be seen in blue eyes as well as in grey eyes.

No albinos were met with in the material examined by me, and my observations, therefore, relate to pigmented eyes only.

It has generally been supposed that the various types of eye-colours grade into each other without sensible breaks of continuity. A critical examination, however, shows that there is a distinct discontinuity between:

(1) The eyes in which two kinds of pigments are present; the one, yellow-brown in colour, deposited on the outer or anterior surface of the iris; the other, blue-black in colour, deposited on the inner or posterior surface of the iris. Such eyes I propose to call *duplex*.

(2) The eyes in which the posterior pigment alone is present in the iris, the anterior pigment being absent. Such eyes may be called *simplex*. The application of popular names to these types is uncertain and quite unreliable; but, in general, eyes that would be called brown belong to the duplex type, while many of the blues and some of the greys belong to the simplex type.

(1) THE DUPLEX TYPE.

To the duplex type belong the various shades of eyes with both anterior and posterior pigments.

In my observations, three distinct patterns of duplex eyes were found, viz.:

(a) The *self-coloured duplex*, in which the anterior pigment is

distributed over the whole front of the iris, practically obscuring the posterior pigment as in ordinary brown eyes.

(b) The *ringed* duplex, in which the anterior pigment is confined to a ringed area round the pupil, leaving the ground colour of posterior pigment clearly exposed round the periphery of the iris.

(c) The *spotted* duplex, in which the anterior pigment is broken up into distinct blotches or spots irregularly scattered over the posterior pigment which forms the ground colour.

Self-coloured duplex eyes vary in shade, presenting different grades of anterior pigmentation. In the darker brown shades the anterior pigment is more densely deposited than in the lighter green shades, the green effect being produced by a thin layer—or in some cases merely a fine irroration—of yellow pigment above the blue posterior layer.

Ringed duplex eyes similarly vary in shade, presenting different grades of anterior pigmentation. In my experience, the distribution of anterior pigment is always denser immediately round the pupil, both in self-coloured and ringed duplex eyes. Eyes with a ring of anterior pigment round the periphery of the iris, but without anterior pigment round the pupil, were not found in my observations.

Spotted duplex eyes also present different grades of anterior pigmentation. The pigmented areas also vary in size and number in different individuals and in the two eyes of the same individual.

Low-grade forms of the ringed duplex pattern are apparently numerous: under ordinary observation these might no doubt pass as blue or grey simplex eyes, the small pigmented ring so blending with the dark pupil as to be unrecognised at a short distance.

Similarly, low-grade forms of the spotted duplex pattern would also pass as blue or grey simplex eyes at a short distance. In both cases, however, a closer inspection reveals their true nature.

In carrying out my observations, I found that about one-half, of eyes, which appeared to be simplex when viewed in the ordinary way, were really duplex when closely examined in a good light with a lens.

Eyes presenting grades of anterior pigmentation so low that they can be mistaken for simplices have not occurred in my experience, and if such eyes do occur, they must be extremely rare in the population which I have studied.

In duplex eyes the anterior pigment is visible soon after birth, so that quite young infants are included in my observations. That anterior pigmentation tends to increase with age in young children is evident from the results of my observations during three years,

though to what extent is not yet clear, owing to the limited period of observation.

(2) THE SIMPLEX TYPE.

To the simplex type belong the various shades of eyes with posterior pigment only, the anterior pigment being quite absent, as in all clear blue and clear grey eyes.

The darker shades of blue are apparently due to the greater delicacy and transparency of the fibrous tissues of the iris through which the posterior pigment is seen, while the lighter shades of blue and the coarser greys seem to be due to the greater coarseness and opacity of the same tissues.

These structural differences appear to be continuous, a series of intermediate blue-greys linking up the finer blues with the coarser greys.

A further complication arises from the fact that, in most cases, the finer tissues of the iris become coarser with age, and young children with dark blue eyes may mature into adults with light blue, blue-grey, or grey eyes.

I have found striking illustrations of this in large families, where a whole series of shades from blue to grey were seen, the younger children being blue and the older ones grey. Consequently, no attempt has been made to distinguish between the many shades of clear blue and clear grey eyes, but all eyes with posterior pigment only are classed as simplex.

Finally, the clear blue and clear grey simplex eyes, with no trace of anterior pigment, must be carefully distinguished from the numerous low-grade duplex eyes, previously noted, which are often called "blue" or "grey."

HEREDITY OF THE DUPLEX AND SIMPLEX TYPES.

All families with less than two children are omitted, and families of two were not taken freely. At first, the largest families available were selected but afterwards it seemed desirable to study collaterals, consequently some small families are included.

Out of the 139 families observed, 20 were simplex matings, 50 were duplex matings, and 69 were duplex-simplex matings.

SIMPLEX MATINGS.

The 20 matings of simplex females with simplex males produced 101 offspring, all of the simplex type. Table I gives the numbers found in each family. Each family is distinguished by the number and initials of the male parent:

TABLE I.

Simplex \times Simplex.

No. and initials of σ parent	Duplex	Simplex	Total offspring
15 A. F.	0	4	4
27 J. T.	0	12	12
31 D. N.	0	11	11
89 J. M.	0	3	3
91 S. H.	0	3	3
93 F. G.	0	12	12
97 H. C.	0	6	6
101 J. L.	0	7	7
105 T. S.	0	4	4
113 E. D.	0	2	2
133 W. D.	0	4	4
137 J. C.	0	7	7
217 J. A.	0	4	4
221 J. D.	0	2	2
231 W. K.	0	5	5
235 A. B.	0	7	7
243 J. F.	0	2	2
255 J. H.	0	2	2
257 J. C.	0	2	2
277 A. A.	0	2	2
20	0	101	101

DUPLEX MATINGS.

The 50 matings of duplex females with duplex males gave two kinds of results: (a) 37 families produced 195 offspring, all of the duplex type; (b) 13 families produced 63 offspring, of which 45 were duplex and 18 simplex. Table II (a) and (b) give the numbers found in each family.

TABLE II.

Duplex \times Duplex.

No. and initials of σ parent	Duplex	Simplex	Total offspring
(a) Giving all Duplex			
5 W. H.	8	0	8
13 J. C.	2	0	2
33 T. S.	8	0	8
39 J. P.	6	0	6
41 W. H.	7	0	7
43 G. L.	6	0	6
55 J. B.	10	0	10
57 J. B.	3	0	3
59 C. B.	12	0	12
65 J. F.	7	0	7
69 B. H.	5	0	5
71 R. E.	6	0	6
73 A. S.	6	0	6
81 T. C.	9	0	9
83 J. W.	3	0	3
85 W. P.	4	0	4
103 H. E.	5	0	5
117 C. H.	6	0	6
123 J. S.	4	0	4
129 J. W.	8	0	8
131 J. G.	6	0	6
135 T. W.	4	0	4
139 J. B.	3	0	3
141 M. C.	2	0	2
145 W. P.	2	0	2
161 J. M.	5	0	5
173 B. B.	10	0	10
177 F. S.	2	0	2
191 E. G.	4	0	4
211 T. R.	2	0	2
215 C. W.	3	0	3
223 H. G.	4	0	4
237 G. K.	4	0	4
259 G. G.	3	0	3
265 J. R.	5	0	5
269 W. P.	3	0	3
275 A. P.	8	0	8
37	195	0	195

TABLE II—*continued*

No. and initials of ♂ parent	Duplex	Simplex	Total offspring
(b) Giving Duplex and Simplex			
107 W. S.	1	1	2
111 J. W.	2	1	3
115 T. B.	3	1	4
165 E. E.	5	1	6
169 G. B.	5	1	6
219 J. R.	5	1	6
227 E. H.	2	1	3
249 H. H.	6	2	8
253 A. F.	3	2	5
261 J. M.	4	2	6
263 A. N.	3	3	6
267 E. D.	3	1	4
271 W. W.	3	1	4
13	45	18	63

DUPLEX-SIMPLEX MATINGS.

The 69 matings of duplex and simplex parents also gave two kinds of results: (a) 17 families produced 66 offspring, all of the duplex type; (b) 52 families produced 258 offspring, of which 121 were duplex and 137 were simplex.

Table III (a) and (b) give the numbers found in each family.

TABLE III.

Duplex × Simplex.

No. and initials of ♂ parent	Duplex	Simplex	Total offspring
(a) Giving all Duplex			
9 S. E.	2	0	2
45 J. H.	8	0	8
53 D. A.	2	0	2
67 J. H.	9	0	9
77 M. G.	3	0	3
121 L. C.	4	0	4
125 E. R.	3	0	3
143 W. D.	4	0	4
147 W. B.	2	0	2
167 T. C.	7	0	7
181 J. B.	5	0	5
201 E. A.	3	0	3
205 W. B.	4	0	4
209 J. H.	2	0	2
213 J. K.	2	0	2
239 H. C.	3	0	3
245 J. T.	3	0	3
17	66	0	66

TABLE III—continued

No. and initials of ♂ parent	Duplex	Simplex	Total offspring
(b) Giving Duplex and Simplex			
1 C. H.	3	2	5
3 G. F.	0	6	6
7 W. E.	3	5	8
17 W. J.	1	1	2
19 F. B.	3	1	4
21 J. B.	4	5	9
23 T. P.	0	4	4
25 R. B.	2	3	5
29 A. F.	5	5	10
35 R. C.	3	4	7
37 S. E.	4	2	6
47 J. S.	3	3	6
49 T. K.	2	2	4
51 G. D.	1	2	3
61 T. C.	5	1	6
63 T. L.	4	5	9
75 J. A.	2	3	5
79 W. W.	4	3	7
87 J. B.	5	4	9
95 J. R.	4	5	9
99 C. C.	5	4	9
109 W. P.	1	1	2
119 J. T.	2	4	6
127 G. S.	3	1	4
149 H. T.	1	4	5
151 W. R.	5	2	7
153 J. M.	3	3	6
155 W. N.	1	1	2
157 T. L.	3	3	6
159 W. H.	4	1	5
163 W. H.	3	3	6
171 D. S.	4	3	7
175 J. C.	2	3	5
179 G. G.	1	1	2
183 W. E.	1	1	2
185 R. S.	2	3	5
187 R. A.	1	1	2
189 G. K.	2	4	6
193 T. C.	1	2	3
195 J. P.	3	1	4
197 J. P.	1	1	2
203 A. P.	1	2	3
207 J. L.	1	1	2
225 C. H.	3	1	4
229 J. N.	1	2	3
233 J. B.	0	4	4
241 J. R.	2	3	5
243 J. F.	2	1	3
247 J. H.	0	2	2
251 A. B.	2	3	5
273 J. P.	2	1	3
279 E. C.	0	4	4
52	121	137	258

With regard to the heredity of the duplex and simplex types, the above tables show that:

- (1) Simplex parents mated together give all simplex offspring.
- (2) Duplex parents mated together give either (a) all duplex offspring, or (b) duplex and simplex offspring in the proportion of about 3 : 1.
- (3) Duplex parents mated with simplex parents give either (a) all duplex offspring, or (b) duplex and simplex offspring in the proportion of about 1 : 1. It is evident, therefore, that the simplex type, in heredity, behaves as a Mendelian recessive to the duplex type, which is dominant. We have already seen that the duplex type differs from the simplex type by the presence of anterior pigment in the iris.

The unit-characters concerned in the heredity of the duplex and simplex types of eyes are, therefore, presence (duplex) and absence (simplex) of anterior pigment in the iris, presence being dominant over absence which is recessive.

The duplex parents in Tables II (b) and III (b) are all obviously heterozygous, carrying the simplex character in a recessive state.

The duplex parents in Table II (a) and III (a) may be either homozygous or heterozygous.

The duplex parents in Table III (a) with large families are almost certainly homozygous, but in those with small families the numbers of offspring are insufficient to test adequately the gametic constitution of the duplex parents. Similarly in the case of the large families in Table II (a), one of the duplex parents is almost certainly homozygous, while the other parent may be either homozygous or heterozygous.

In the small families the numbers of offspring are again too small to test adequately the gametic constitution of the duplex parents.

In proof of this we have the fact that in Table III (a) each of the three duplex parents of families 53 D. A., 125 E. R., and 209 J. H. is known to have a simplex parent and consequently must be heterozygous, though none of them has yet produced simplex offspring. Similarly in Table II (a) both duplex parents of family 13 J. C. are known to have a simplex parent, though they have not yet produced any simplex offspring. As might be expected in a mixed population, some of the simplex parents observed are known to have been extracted from a duplex parent, or to have had duplex brethren.

For instance, in Table I, at least one of the simplex parents of families 15 A. F., 97 H. C., 231 W. K., 255 J. H., and 257 J. C. is known to have a duplex parent, while of the families 31 D. N. and 243 J. F. one parent at least has duplex brethren.

In accordance with the Mendelian principles, the extracted simplex type breeds true to the simplex character without reversion to its duplex ancestors. In view of recent Mendelian experiments with plants and animals, it did not seem impossible that some simplex individuals at least might be carrying factors which on meeting, in the process of fertilisation, with other complementary factors, might give rise to reversions of the duplex type, but, so far, no such cases have been found. For the present, therefore, while remembering such a possibility, we must take it that the duplex and simplex type of eye-colour in man constitute a simple Mendelian case of presence and absence of a certain pigment.

With regard to the different patterns of duplex eyes and their various shades, my facts, so far, do not enable me to determine positively their genetic relations. The chief difficulty is due to the fact that the anterior pigment present in children tends to increase with age, though to what extent, or to what age, is not yet known, owing to the limited period of observation.

In the few families observed, with all adult offspring, the evidence suggests that the ringed pattern is recessive to the self-coloured pattern, which is dominant; but with regard to the genetic relations of the spotted pattern to the ringed and self-coloured patterns there is practically no evidence available.

PREVIOUS WORK.

Large numbers of records of eye-colours have been compiled and discussed by anthropologists and biometricians at home and abroad. In most cases, however, the data relate to certain sections of the population, such as school children and conscripts, not analysed or grouped according to their families. So far, I have found only two memoirs which approach the question of the inheritance of eye-colour in man by a comparison of parents with their offspring. The first is that of Alphonse de Candolle¹.

De Candolle, with the assistance of some 28 experienced observers, collected a number of records of the inheritance of eye-colours in Switzerland, Germany, and Sweden. De Candolle made two classes of eye-colours, "brown" and "blue," omitting all doubtful shades. The "brown" class included "black," "brown," "yellow-brown," and "green-brown." The "blue" class included "blue," "blue-grey," "grey,"

¹ "Hérédité de la Couleur des Yeux dans l'Espèce Humaine," *Archives des Sciences*, Genève (3ème période, XII. 1884, pp. 97—119).

"green-blue," and "green^a-grey." Comparing de Candolle's classes and shades with mine, it is evident that all the "brown" class belong to the duplex type with anterior pigment, but that only part of the "blue" class belong to the simplex type, without anterior pigment.

The second memoir is that of Mr Francis Galton¹. Mr Galton collected a number of records of family eye-colours in the British Isles, among the "Records of Family Faculties"—known as the R.F.F. data. These family records were obtained through the offer of prizes to the public².

From the family records sent in, Mr Galton made three classes of eye-colours, "light," "hazel," and "dark." The "light" class included the shades recorded as "light blue," "blue," "dark blue," "grey," and "blue-green." The "hazel" class included "dark grey" and "hazel." The "dark" class included "black," "very dark brown," "dark brown," "brown," and "light brown." Comparing the shades of colour sent in to Mr Galton by his correspondents with mine, it is evident that all of Mr Galton's "dark" class belong to the duplex type with anterior pigment. With regard to the "hazel" class, part of these would probably represent my ringed duplex pattern, while the remainder might belong either to the duplex or simplex type, according to the interpretations of the colours by different observers. Mr Galton apparently regards "dark grey" and "hazel" as bicolor eyes³, which would make them practically equivalent to my ringed duplex eyes. In view, however, of my experience with popular descriptions of eye-colours, it is highly probable that many of Mr Galton's correspondents would record certain forms of self-coloured duplex eyes as "hazel," and certain forms of "simplex" eyes as "dark grey." Mr Galton's "light" class would apparently consist partly of the simplex type without anterior pigment, and partly of the low-grade forms of the duplex type with some anterior pigment. In the nature of the circumstances in which the R.F.F. data were recorded, it cannot, of course, be expected that the observations were critical in regard to the presence or absence of anterior pigment in the iris. On the whole, therefore, it does not seem possible to express either de Candolle's or Mr Galton's classes and shades of eye-colours in terms of duplex and simplex pigmentation. It was on Mr Galton's R.F.F. data that Professor Karl Pearson based his memoir "On the

¹ "Family Likeness in Eye-colour," *Roy. Soc. Proc.* 1886, XL. No. 245, pp. 402—416.

² See *Natural Inheritance*, 1889, pp. 72—78.

³ *Loc. cit.* pp. 142, 144.

Inheritance of Eye-colour in Man¹," and afterwards concluded that nothing corresponding to Mendel's principles appeared in the characters for eye-colour in man².

SUMMARY.

An examination of the eye-colours of a number of parents and their offspring in a Leicestershire village shows that there are at least two discontinuous types of iris in man:

(1) The duplex type, with both anterior and posterior pigments, as in ordinary brown eyes.

(2) The simplex type, with posterior pigment only, the anterior pigment being absent, as in clear blue eyes.

In heredity the simplex type behaves as a Mendelian recessive to the duplex type, which is dominant. The unit characters concerned are evidently presence (duplex) and absence (simplex) of anterior pigment on a basis of posterior pigment, presence being dominant.

The duplex and simplex types can be distinguished at any age. Various pigmental and structural changes take place in the iris during childhood and youth, the extent of which is not yet known. Few families with living parents and offspring, all adult, are to be found in one village. Consequently, it has not yet been possible to determine the genetic relations between the various shades of the duplex type.

NOTE. I desire to acknowledge my indebtedness to Mr W. Bateson for some valuable criticisms and suggestions in regard to the preparation of this paper, and also to Mr R. C. Punnett, who came down and examined a number of the simplex eyes recorded above.

(NOTE ADDED 11th January, 1908.)

Since the above paper was presented, an article on "Heredity of Eye-colour in Man" has appeared in *Science*, 1907, xxvi, pp. 589-592 (dated 1st November), in which Professor C. B. Davenport independently arrives at similar conclusions, pointing out the Mendelian inheritance of eye-colour in man.

¹ *Phil. Trans. A*, 1900, cxcv. p. 102.

² *Biometrika*, 1903, II, pp. 213, 214.

XX

BRITISH ASSOCIATION

FOR THE

ADVANCEMENT OF SCIENCE.

LEICESTER MEETING, 1907¹.

(*Section D—Zoology, and Section K—Botany.*)

Visit to Burbage to see the Heredity Experiments and a Demonstration of the Inheritance of Eye-colour in Man (fig. 100).

FRIDAY, *August 2*, 1907.

For this purpose there were assembled about 100 school children belonging to the families studied. In these investigations two discontinuous types of eye-colours have been found.

(a) Eyes with brown pigment in various amounts on the front of the iris, called **Duplex**.

(b) Eyes with no brown pigment on the front of the iris, called **Simplex**.

Duplex and Simplex eyes follow Mendel's Law of heredity, duplex being dominant and simplex recessive. The unit characters concerned are presence and absence of the brown anterior pigment of the iris. The blue-black posterior pigment of the iris is present in both duplex and simplex eyes.

In the schools the children were arranged in three groups:

(1) **Duplex matings with all duplex children**, representing pure dominants (DD).

(2) **Duplex matings with both duplex and simplex children**, representing hybrid dominants (DR) and illustrating Mendelian segregation.

¹ Extracted from the printed programme of the visit to Burbage of Sections D and K of the British Association Leicester Meeting, 1907. (See also *Nature*, 1907 (Sept. 26), LXXVI. p. 558.)

(3) **Simplex matings with all simplex children**, representing pure recessives and illustrating gametic purity.

(The duplex children wore red and the simplex children blue rosettes.)

The following heredity experiments were also seen :

(1) **Sweet Peas**, illustrating Mendelian segregation and gametic purity of colour characters in F_2 and F_3 .

(2) **Rabbits**, illustrating the hereditary transmission by albinos of hidden factors which can determine the quality of colours and their distribution on the body.

XXI

MENDEL'S LAW OF HEREDITY AND ITS APPLICATION TO MAN¹

A few years ago the scientific world was startled by the discovery of Mendel's Law of Heredity. Since then, the law has been tested again and again, by many experimenters in many lands, and has been found to apply to various kinds of plants and animals. In my own experiments and observations, for instance, the Mendelian phenomena of dominance, segregation, and purity have been witnessed in peas, poppies, sweet peas, antirrhinums, primulas, tomatoes, orchids, and other plants, as well as in poultry, rabbits, and horses. In view of these facts, it seemed natural to expect that the Mendelian phenomena would also be found in Man.

In the case of Man, however, direct experiment was obviously impracticable, so that recourse was had to the observation of the inheritance of human characters in individual families.

Fortunately, suitable material lay close at hand in my native village, and so far, about 200 families, whose members and history are well known to me, have been observed and studied during the past four years. The inhabitants themselves have entered willingly into the spirit of the affair, and have given me every facility to pursue my investigations, for which I am duly grateful.

The essence of Mendel's discovery was that each characteristic—or character as it is termed—may be inherited separately and independently.

Mendel has taught us to recognise that the true unit of heredity is not the individual, but the single character.

Perhaps the most obvious of the physical characters in man is the colouring or pigmentation of the eyes and hair, and it was to this that I first directed my attention. In the course of my investigations, it soon became apparent that the colouring of the eyes and hair was not

¹ Abstract of a lecture delivered before the Leicester Literary and Philosophical Society, Feb. 10th, 1908, and reprinted from *Trans. Leic. Lit. and Phil. Soc.* xii. Pt. 1, pp. 35-48 (1908).

always coupled in inheritance, but that each was often inherited independently of the other. Thus light eyes with dark hair, and dark eyes with light hair, were frequently met with. It seemed, therefore, necessary at the outset, to deal with the colouring of the eyes and hair separately. We will, consider first the question of Eye-colour.

EYE-COLOUR.

In a paper communicated to the Royal Society in May, 1907, I showed that two distinct types of eyes may be recognised, *Duplex* and *Simplex*.

Both duplex and simplex eyes have black pigment behind the iris, but duplex eyes have also brown or yellow pigment in front of the iris, while in simplex eyes this pigment is quite absent. An examination of the Burbage families showed that when both parents had simplex eyes, all the children were simplex, however mixed the ancestry might have been.

TABLE I (EYE-COLOUR).

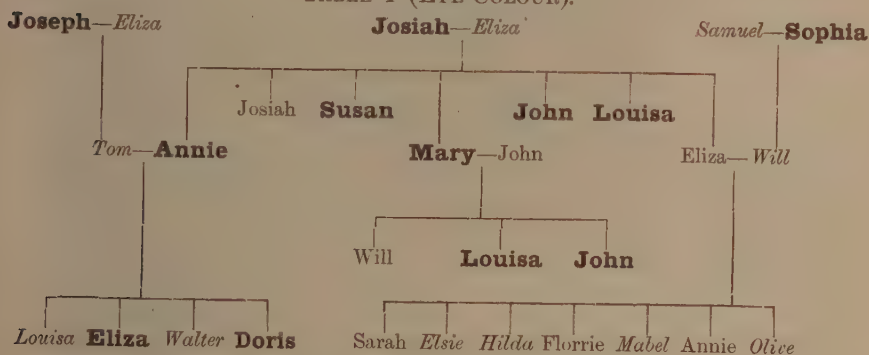
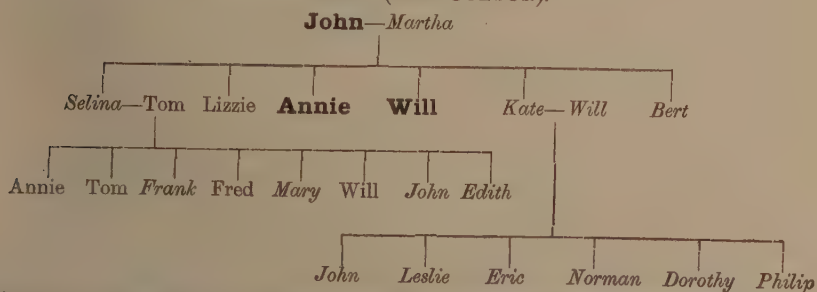


TABLE II (EYE-COLOUR).



Pedigrees of Burbage families to illustrate the Mendelian inheritance of Eye-colour.
(Names in black type are Self Duplex, ordinary type are Ringed Duplex, italics are Simplex.)

When both parents had duplex eyes, *either*, all the children were duplex, *or*, most of them were duplex while a few were simplex. When one parent was duplex, and the other simplex, then, *either*, all the children were duplex, *or*, about one-half were duplex and one-half simplex.

This evidence showed that duplex and simplex eyes follow Mendel's law of heredity, duplex being dominant and simplex recessive.

At the meeting of the British Association at Leicester in August 1907, thanks to the courtesy of Sections D and K, I was able to demonstrate the above results, with the aid of about 100 of the Burbage school children.

Duplex eyes appear to be of three distinct patterns, self-coloured, ringed, and spotted. My investigation of the heredity of these duplex patterns is not yet completed, but so far, the evidence suggests that the self pattern with more pigment, is dominant over the ringed pattern with less pigment which is recessive.

It is interesting and satisfactory to note that Professor C. B. Davenport, Director of the Carnegie Station for Experimental Evolution, New York, has also independently arrived at the conclusion that eye-colour in man is inherited according to Mendel's Law (*Science*, xxvi. pp. 589—592; Nov. 1, 1907). Professor Davenport makes three classes of eye-colours, "brown," "grey," and "blue." "Brown" being dominant over "grey" and "blue," and "grey" dominant over "blue."

I see no objection to these categories, if it is clearly understood that "brown" represents the self duplex, "grey" the ringed duplex, and "blue" the simplex type.

The chief difficulty in adopting the popular terms, as I have already pointed out elsewhere, is that eyes which are generally known as "grey" and "blue," may be either duplex or simplex according to the presence or absence of pigment in front of the iris. Another serious difficulty is that the spotted duplex, which appears to belong to the "grey" category, behaves quite differently in heredity from the ringed duplex.

HAIR-COLOUR.

Of the many shades of human hair-colour, perhaps the most distinct and definite is that known as "fiery red."

The sporadic occurrence of red hair in families is a matter of common knowledge, and at once suggests the probability of the character being a Mendelian recessive. A careful examination of the parents and pedigrees of the red-haired children in Burbage, has so far confirmed that

expectation. For when both parents had red hair, all the children were red. So far, however, only a few families with both parents red, have been found, the mating of red with red being apparently unpopular.

TABLE III (HAIR-COLOUR).

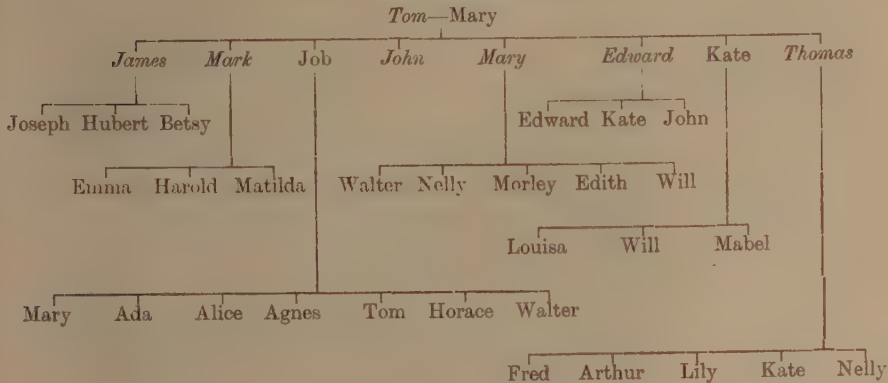


TABLE IV (HAIR-COLOUR).

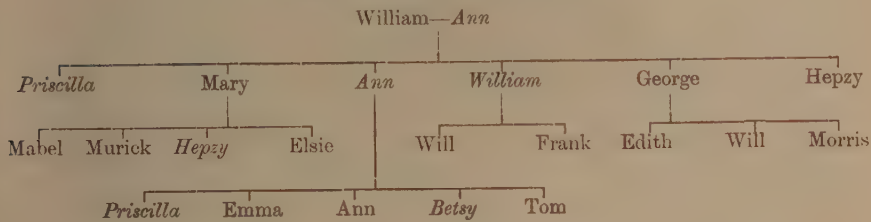
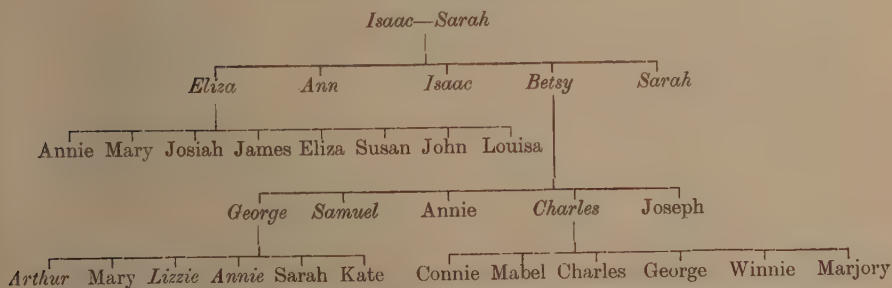


TABLE V (HAIR-COLOUR).



Pedigrees of Burbage families illustrating the Mendelian inheritance of Hair-Colour.
(The names in ordinary type have Brown Hair, those in italics have Red Hair.)
All the parents omitted have Brown Hair.

When both parents had brown hair (including light and dark brown), *either*, all the children were brown, *or*, most of them were brown and a few were red.

When one parent was brown and the other red, *either*, all the children were brown, *or*, about one-half were brown and one-half were red.

These results suggest that brown and red hair follow Mendel's law of heredity, brown being dominant and red recessive.

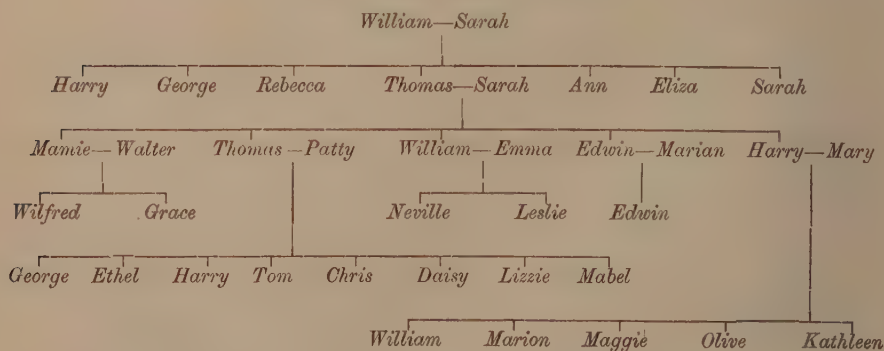
In certain cases, however, which seem to be rare, the dominance of brown over red is not always complete, the hybrid form sometimes showing distinct traces of red in the brown. These hybrid reds, however, are easily distinguished from the pure fiery reds which show no trace of brown.

MUSICAL SENSE.

That some people have a natural disposition for music, while others have not, is evident to the most casual observer. That this natural disposition, temperament, faculty, or sense—whatever it may be called—is innate and hereditary there can, I think, be little doubt. Musical associations and training can, of course, do much in enriching the musical qualities in a person of musical disposition, but in the absence of the musical sense these extraneous stimuli are comparatively powerless.

No doubt there are many cases where by persistent effort and constant practice, under careful tuition, individuals without the musical sense may succeed in learning to play a more or less mechanical

TABLE VI (MUSICAL SENSE).



Pedigree of a Burbage family. ALL the members Musical.

TABLE VII (MUSICAL SENSE).

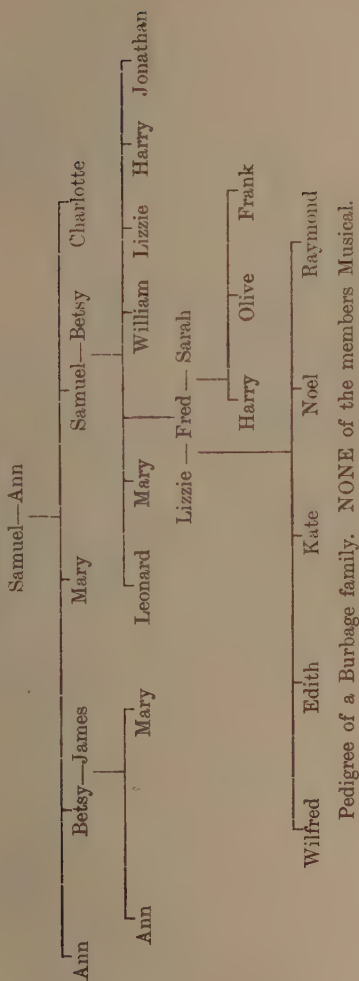
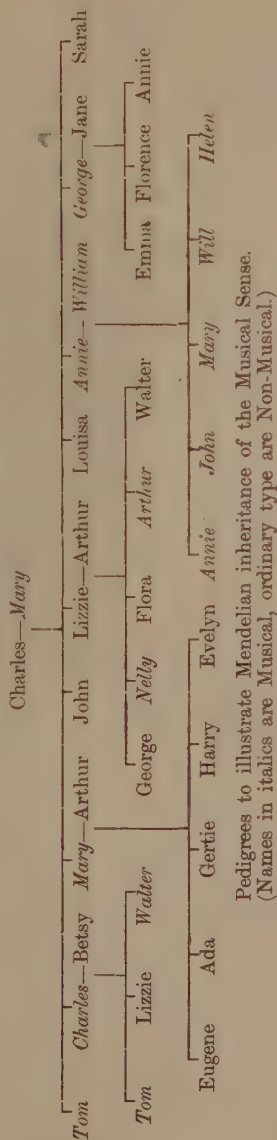


TABLE VIII (MUSICAL SENSE).



instrument, like the pianoforte, but in the absence of the innate faculty for music, they would be "dull musicians" at the best, and could not be considered musical in the true sense of the word. It is extremely doubtful, for instance, whether anyone without the musical sense could ever learn to sing or play the violin, tunefully. On the other hand, many people, with no musical associations or training, display a musical nature quite early in life. I think that it will be generally admitted that when the musical sense is present in an individual, it manifests itself naturally by responding to any musical stimulus with which it comes in contact. This is the test that I have adopted in separating the musical from the non-musical. Those individuals who have displayed the presence of the musical sense have been classed as musical, while those who have not have been regarded as non-musical.

A remarkable case of the inheritance of the musical sense was found in one of the Burbage families, in which all the members for three generations were musical, all were natural singers and most of them have sung in the Church choir. As a contrast to this in another family in three generations, not one individual was musical.

Further investigation showed that when both parents were musical, all the children were musical. When neither parent was musical, *either*, none of the children was musical, *or*, a few were musical and most of them were not. When one parent was musical and the other not, *either*, none of the children was musical, *or*, about one-half were musical and one-half were not. These observations suggest that the musical sense is a Mendelian character, recessive to the non-musical character which is dominant.

HEREDITARY DISEASES.

The important question of the inheritance of human diseases is a difficult one for a layman to approach. So much depends on the diagnosis, and where doctors may differ a mere naturalist hesitates to intervene. In many cases too, it seems doubtful whether certain diseases, generally presumed to be hereditary, can be strictly described as such in the modern biological sense of the word. So far, I have not ventured to deal with this question in the Burbage population. There are, however, on record two cases of Mendelian inheritance of abnormal conditions in man, which seem to be sufficiently clear and established to repeat. The first is the case of a family in Pennsylvania, described by Dr Farabee. In this family many individuals had deformed digits, the fingers and toes having two phalanges instead of three, the affected

members being also of very short stature. This abnormal character behaved as a Mendelian dominant over the normal character which was recessive. When one parent was abnormal and the other normal—the usual mating—about one-half of the children were affected, and one-half were free from the deformity. When both parents were normal, all the children were normal, notwithstanding their descent from abnormal ancestors. The other case is that of the Nougaret family of Vendémian near Montpellier, many members of which suffered from a particular form of night-blindness. Mr E. Nettleship has kindly sent me a remarkable pedigree of this family, embracing ten generations from 1637—1907, and consisting of more than 2,000 individuals.

In this case, too, the disease behaves as a Mendelian dominant to the healthy condition which is recessive. When one parent was diseased and the other healthy—the usual mating—about one-half of the children were night-blind and one-half were healthy. When both parents were healthy, all the children were healthy, notwithstanding their descent from night-blind ancestors. Altogether, there were about 1,630 healthy individuals descended from the original diseased stock. Among these are included a large number that have remained healthy and free from night-blindness for seven generations.

When both parents were night-blind (a single case only), the two children were both night-blind, as was to be expected.

The above evidence shows that Mendel's law of heredity applies to man in the same way that it applies to plants and animals. So far, only a beginning has been made in the discovery of Mendelian characters in man. The science of heredity in man is yet in its infancy, but thanks to the discovery of Mendel's law, a beginning has been made, and we look to the future with high hopes. With a knowledge of Mendel's law, it is possible to foretell, to a certainty in many cases, what Mendelian characters will appear in the offspring of two parents, and in what proportions these will be likely to appear.

The practical value of this knowledge depends entirely on its application. That delicate question, I must leave to your imagination.

XXII

INHERITANCE OF ALBINISM IN ORCHIDS¹

In consequence of the important results recently obtained at Cambridge by Professor Bateson, Mr Punnett and Miss Saunders in their Mendelian experiments with Sweet Peas and Stocks, the question of the inheritance of albinism has become one of great biological interest.

In Orchids, the raising of albino forms from seed is also of much practical interest. It may be useful therefore to collect in a brief note what has already been done by Orchid breeders in this direction.

Albino Orchids may be provisionally divided into two classes:— (1) True albinos with no trace of purple sap. (2) Tinged "albinos" with some purple sap.

The following list gives the results so far obtained in mating (*a*) true albinos with true albinos, (*b*) tinged "albinos" with tinged "albinos," (*c*) tinged "albinos" with true albinos. The records have been taken partly from the reports of the meetings of the *Roy. Hort. Soc.*, partly from Mr Rolfe's notes in the *Orchid Review*, and partly from personal notes and correspondence with Orchid breeders. The nomenclature adopted is that of the *Orchid Stud Book*, now being issued from the press².

I trust that the list is fairly complete, and I hope that any omissions will be at once supplied by Orchid breeders.

(A) TRUE ALBINOS × TRUE ALBINOS.

Paphiopedilum callosum Sanderæ, selfed by Mr Norman Cookson, produced true albinos. Another batch, raised by Mr T. Statter, also produced true albinos (fig. 101).

P. Lawrenceanum Hyeatum, selfed by Mr Norman Cookson, produced nine plants, eight of which reproduced the true albino, while one plant is said to have reverted to an ordinary coloured form of *P. Lawrenceanum*. This apparent exception is remarkable, and a repetition of this experiment with larger numbers would be useful (fig. 58).

¹ Reprinted from *Gard. Chron.* 1909, I. pp. 81–82.

² *The Orchid Stud-Book: an Enumeration of Hybrid Orchids*, by R. A. Rolfe and C. C. Hurst. 327 pp., 120 figs, Kew (*Orchid Review*) 1909.

P. Lawrenceanum Hyeannum × *P. callosum Sanderæ*, raised by Messrs Charlesworth, in 1900, produced the albino hybrid *P. × Maudiae*, all the plants of which have so far proved to be true albinos. Another batch raised by Baron Schröder in 1907 also produced true albinos (fig. 102).

P. × Maudiae × *P. insigne Sanderianum* (fig. 103), raised by Colonel Holford in 1908, produced the albino hybrid *P. × Rosettii*, 16 plants of which have so far flowered, all apparently true albinos. It may be noted here that while *P. insigne Sanderianum* so far appears to behave as a true albino, yet the presence of some dark-coloured hairs at the base of the petals suggests that this variety may possibly be a tinged albino like *P. insigne Sanderæ*. It would be interesting to know if the hybrid *P. × Rosettii* also has those dark-coloured hairs (fig. 104).

P. callosum Sanderæ × *P. bellatulum album* (fig. 105), raised by Mr Cookson in 1907, produced the coloured hybrid *P. × Wottonii*, 25 plants of which have flowered, all apparently sap-coloured like the typical hybrid between *P. callosum* and *P. bellatulum*.

P. Lawrenceanum Hyeannum × *P. bellatulum album*, raised by Mr Cookson, produced the coloured hybrid *P. × Lawrebel* resembling the typical hybrid between *P. Lawrenceanum* and *P. bellatulum*.

Cattleya Mossiae Wageneri, selfed by Messrs Charlesworth in 1907, produced a true albino with no trace of sap colour (fig. 106).

C. Mossiae Wageneri × *C. Gaskelliana alba*, raised by M. Jules Hye, produced three true albinos, viz., *C. × Hyeæ*, *C. × H. Suzanne*, and *C. × H. Jungfrau* (fig. 107).

C. Mossiae Wageneri × *C. intermedia alba*, raised by Colonel Folford, in 1906 produced the albino hybrid *C. × Mackayi Undine*, 14 plants of which flowered true albinos. In 1908 three true albinos of the same parentage were exhibited by Mr R. G. Thwaites, also one by Sir Trevor Lawrence and one by Messrs Veitch (fig. 114).

C. Schröderæ alba × *C. intermedia alba* (figs. 112 and 113), raised by Mr Cookson, produced in 1907 the coloured hybrid *C. × Thayeriana*, similar to the hybrid raised by Mr Orpet between the typical *C. intermedia* and *C. Schröderæ alba*.

C. Gaskelliana alba × *C. Harrisoniana alba* (figs. 108 and 110), exhibited by Mr Thwaites in 1908, produced the coloured hybrid *C. × Williamsiae*, four plants of which had coloured flowers like the typical hybrid between *C. Gaskelliana* and *C. Harrisoniana*.

C. Gaskelliana alba × *C. Warneri alba* (figs. 108 and 111), raised by M. Peeters and exhibited in 1904, produced the hybrid *C. × Peetersiae*, five of which were true albinos with pure white flowers and green leaves,

and two were coloured, having lilac-purple flowers with purple margins to the leaves¹.

C. Eldorado alba × *Laelia Perrinii alba*, according to a record in *Rev. Hort.* 1907, p. 31, produced coloured offspring bearing pink flowers.

Odontoglossum crispum xanthotes × *O. nobile album*, raised by Messrs Charlesworth, produced in 1908 the hybrid *O.* × *armainvillierense xanthotes*, all of which have so far flowered true albinos.

Dendrobium nobile virginale, selfed by Mr Thwaites, came true from seed. Another batch, consisting of several hundred plants raised from one capsule by Messrs Armstrong and Brown, flowered in 1907 and 1908, and all were true albinos (fig. 115).

(B) TINGED "ALBINOS" × TINGED "ALBINOS."

Paphiopedilum insigne Sanderæ, selfed by Mr Cookson, apparently came true from seed. Other batches raised by Mr R. I. Measures, Messrs Veitch, Mr W. Bolton, and Colonel Holford all apparently came true from seed. It is not recorded, however, whether all these seedlings were tinged "albinos" like the parent, and it may be that some were true albinos (figs. 59 and 103). (See footnote 2, p. 55.)

P. insigne Sanderæ × *P. insigne Dorothy*, raised by Mr Appleton, apparently all reverted to the ordinary type of *P. insigne*, with smaller, and in some cases less numerous, spots. This case is particularly interesting, because both parents have a yellow ground colour, which breeds true selfed in the case of *P. insigne Sanderæ*, but which, when crossed, reverts to the typical green ground colour of *P. insigne*.

P. insigne Sanderæ × *P. aureum Surprise* (figs. 83 and 83A), raised by M. Peeters, in 1908 produced a typical green-coloured, spotted *P. insigne*, while soon afterwards Mr J. H. Craven exhibited a plant of the same parentage bearing a yellow flower. In this connection it may be noted that in 1908 Colonel Holford raised eight plants from *P. insigne Chantinii Lindenii* × *P. insigne montanum aureum*, both with yellow ground colour, and all the seedlings reverted to the green ground colour of the ordinary *P. insigne*.

Cattleya labiata Measuresii × *C. labiata Amesiana*, raised by Mr Thwaites, in 1908 produced a considerable number of plants, all of which bore coloured flowers like the ordinary *C. labiata*.

C. Mossiæ Reineckiana × *Laelia purpurata alba*, raised by M. Peeters, produced both the tinged "albino" *Lælio-Cattleya* × *Canhamiana alba*

¹ These hybrids were individually examined by the late Mr R. A. Rolfe and myself at Brussels in April 1903. (Note added 1925.)



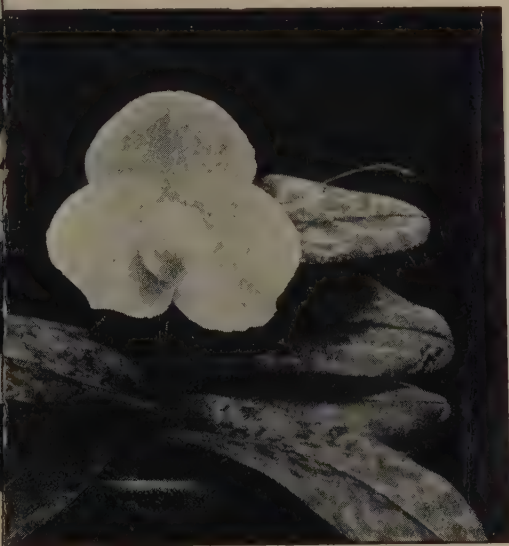
Fig. 101. *Paphiopedilum callosum* Pfitz.

(*Orchid World* albino).

see 3 (fig. 101).)



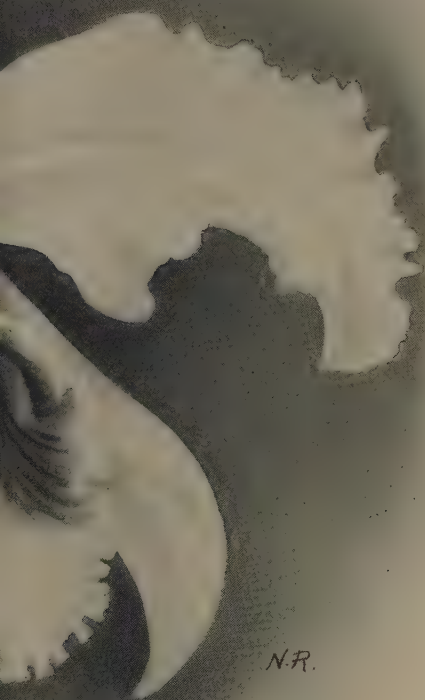
× *Paphiopedilum Rosettii* Hurst
 (× *P. Maudiae* ♂) (RR albinos (figs. 103 and 102)).
 (*Orchid Review*.)



P. bellatulum Pfitz. var. *album* Rolfe (CC albino).
 (*Orchid Review*.)



Fig. 106. *Cattleya Mossiae* Hoo
(*Roy. H*



N.R.

Tageneri O'Brien (RR Albino).
(ourn.)



Fig. 107. × *Cattleya Hyeæ* Rolfe et Hurst var. **Suzanne** Hurst (R.
(Roy.



(*C. Mossiae* Wageneri ♀ (fig. 105) × *C. Gaskelliana* alba ♂ (fig. 108)).
Journ.)



Fig. 108. *Cattleya Gaskelliana* Rehb.
(*Roy. L.*)



N.R.

iams var. **alba** Williams (RR Albino).
(ourn.)




Fig. 109 \times *Cattleya Peetersiae* Rolfe et Hurst var. **Myra** Hurst
(*Roy. H.*)



N.R.



Fig. 110. *Cattleya Harrisoniana* Lindl. var. *alba* Beer.
(CC albino.)



Fig. 111. *Cattleya Warneri* Moore var. *alba* Røebling ex Rolfe.
(Cc albino.)

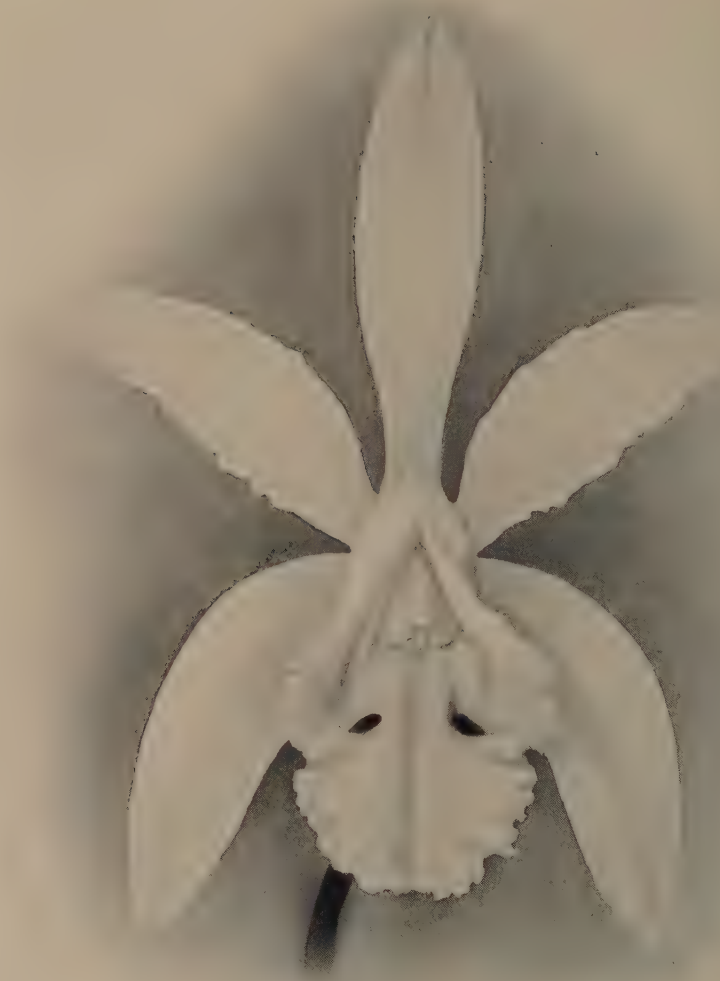


Fig. 113. *Cattleya intermedia* Graham var. **alba** Williams (RR albino).
(*Roy. Hort. Soc. Journ.*)



Fig. 114. \times *Cattleya Mackayi* Rolfe et Hurst var. *Undine* Hurst (RR albino).

(*C. intermedia alba* ♀ (fig. 113) \times *C. Mossie Wageneri* ♂ (fig. 106).)

(*Orehid Review*.)



Fig. 115. *Dendrobium nobile* Lindl. var. *virginale* Rolfe.
200 selfed seedlings which are true albinos.
(*Orchid Review*.)

and the ordinary coloured L.-C. \times Canhamiana from the same capsule in the proportion of about two coloured to one tinged albino.

Dendrobium nobile Ballianum \times *D. nobile murrhiniacum*, raised by Mr Gurney Wilson, produced 150 plants, all of which reverted to the typical colouring of *D. nobile*.

(C) TINGED "ALBINOS" \times TRUE ALBINOS.

Paphiopedilum insigne Sanderae \times *P. callosum Sanderae*, raised by Mr Cookson, produced more than 100 plants, all of which were coloured like the typical hybrid *P. \times Leonæ* (*insigne* \times *callosum*).

P. insigne Sanderae \times *bellatulum album*, raised by Messrs Armstrong and Brown, produced *P. \times Helena Armstrongiæ* (fig. 140), a coloured hybrid less spotted than the typical hybrid *P. \times Helena* (fig. 139) (*insigne* \times *bellatulum*).

P. insigne Sanderae \times *P. Lawrenceanum Hyeanum*, raised by Mr M. Isaac, in 1908 produced a coloured hybrid like the typical *P. \times Eucharis* (*insigne* \times *Lawrenceanum*).

P. insigne Sanderae \times *P. \times Maudiae*, raised by Colonel Holford, in 1901 produced none but coloured forms. A coloured form of the same parentage raised in 1908 by Mr Isaac, resembled light forms of *P. \times Eucharis* and *P. \times Leonæ*.

Lælia anceps alba \times *Cattleya Trianae alba*, raised by M. Peeters, in 1903 produced the tinged "albino" *Lælio-cattleya* \times *Boylei Kerchovæ*. Another plant of the same parentage, raised by Mr Mead, also produced a tinged "albino."

Dendrobium \times *Ellisii album* \times *D. nobile virginale*, raised by Mr Thwaites, in 1907 produced 22 plants, all of which were tinged "albinos," but with more colour than the tinged parent.

GENERAL CONCLUSIONS.

The above facts show that when true albino Orchids are mated together the result may be all albinos, all coloured reversions, or both albino and coloured forms from the same capsule. These results are very similar to those obtained in the Mendelian experiments with Sweet Peas and Stocks at Cambridge. It seems probable, therefore, that the appearance of sap-colour in Orchids, as in Sweet Peas and Stocks, depends on the simultaneous presence of two complementary colour factors. If both the colour factors are present the sap is coloured; if either (or both) is absent the sap is colourless. Thus, the typical coloured forms of *Paphiopedilum callosum*, *P. Lawrenceanum*, *P. insigne*

and *P. bellatulum* may be represented as carrying the two complementary colour factors C and R. The albinos of these species, on the contrary, will be carrying only one of these factors, consequently their sap is colourless. If *P. bellatulum album* be represented as carrying the factor C alone, and *P. callosum* Sanderæ, *P. Lawrenceanum* Hyeannum, and *P. insigne* Sanderianum (if a true albino) be represented as carrying the factor R alone, all the results in *Paphiopedilum* are so far clear. On this interpretation *P. insigne* Sanderianum (if a true albino) may be expected to give albinos when crossed with *P. callosum* Sanderæ or *P. Lawrenceanum* Hyeannum and coloured reversions when mated with *P. bellatulum album*. According to the Mendelian scheme in Sweet Peas there are five different kinds of albinos, and the possible matings between any two of them may give any one of four different results, viz:—(1) All albinos; (2) all coloured reversions; (3) equal numbers of albinos and coloured forms; (4) three albinos to one coloured form.

The coloured reversions when selfed should give, on the average, nine coloured to seven albinos. It seems likely that similar results may be found in Orchids, and the appearance of five albinos and two coloured forms from the same capsule in the cross between *Cattleya Gaskelliana alba* and *C. Warneri alba* is certainly suggestive. From this it will be seen that individual albinos apparently identical may differ in their germinal constitution and, consequently, give different results in breeding. In view of this, it would seem desirable for Orchid breeders to adopt some method of ear-marking individual albinos, whether imported or raised from seed. A distinct name would hardly be convenient for individuals which, to the eye, appear alike, but identification might be assured by putting the name of the importer or raiser in brackets after the name of the albino, together with a number showing the order of its appearance. For instance, the original *Paphiopedilum callosum* Sanderæ was first flowered from an importation by Messrs Sander in 1894, and might, therefore, be called (Sander 1); another individual appeared in an importation by Messrs Low in 1904, and might be called (Low 1), and so on. The hand-raised seedlings of *P. callosum* Sanderæ might be distinguished in the same way, thus (Cookson 1), (Statter 1), and so on. In this way all the individuals of any particular albino could be distinguished for breeding purposes. The same principle might be applied to the tinged "albinos," which are equally interesting in their inheritance. The tinged "albino" *P. insigne* Sanderæ will presumably be carrying both C and R, the dense sap colouring of the ordinary *P. insigne* being reduced to a dilute or ghost form, probably owing to the absence of a

complementary pattern factor. The fact that the ghost form *P. insigne* *Sanderæ* breeds true when selfed, but gives the reversionary dense form when crossed with other kinds of ghost forms like *P. insigne* *Dorothy* and *P. x aureum* *Surprise*, tends to confirm this view, though the evidence is yet hardly conclusive. The fact also of the yellow ground-colour of the flower of *P. insigne* *Sanderæ* breeding true when selfed and giving rise to the reversionary, green ground when crossed with other yellow ground varieties may also have a similar explanation. Further evidence in regard to these cases is necessary and may soon be forthcoming.

It is interesting to note that two such apparently similar forms as *P. insigne* *Sanderæ* and *P. insigne* *Sanderianum* have such a different germinal constitution and give such opposite results in breeding. No doubt albino breeders in future will take care to use *P. insigne* *Sanderianum* as a parent instead of *P. insigne* *Sanderæ*. At the same time, from the biological point of view, it is important to test all the yellow varieties, whether they be true albinos, tinged "albinos" or coloured forms.

XXIII

MENDEL'S LAW OF HEREDITY AND ITS APPLICATION TO HORTICULTURE¹

Mendel's law was founded on simple characters in garden peas. In his experiments Mendel found seven pairs of characters that followed his law, namely:

Rounded and wrinkled seeds.

Yellow and green seeds (cotyledons).

Coloured and white seed-coats.

Inflated and constricted pods.

Green and yellow pods.

Distributed and bunched flowers.

Tall and dwarf stems.

It will be observed that Mendelian characters consist of pairs of contrasts. Mendel found that in each case the two contrasting characters behaved in breeding as "dominants" and "recessives," the first named of each pair being "dominant" and the other "recessive."

For instance, when a pure-bred tall pea was crossed with a pure-bred dwarf pea, the offspring were all tall, no matter which way the cross was made. In Mendelian terms tallness is "dominant" and dwarfness "recessive."

When the tall cross-breds produced seeds by self-fertilisation, Mendel found that the offspring consisted of both tall and dwarfs, and on the average there were three tall to one dwarf.

It will be noted that the "recessive" dwarf character, after "skipping a generation," reappeared in a quarter of the offspring. Mendel found that these extracted dwarfs bred permanently true to the dwarf character, notwithstanding the tallness of their parents and ancestors.

The tall individuals of the same generation, however, proved to be of two kinds; on the average one-third of them were pure tall, breeding true to the tall character, notwithstanding their dwarf ancestors, while

¹ Lecture delivered before the Royal Horticultural Society, May 4th, 1909, and reprinted from *Journ. Roy. Hort. Soc.* xxxvi. Pt. 1, pp. 22-52, figs. 12-34 (1910).

two-thirds of them were impure tall throwing dwarfs as well as tall, as their parents did before them.

The diagram (fig. 116) will serve to illustrate the results obtained by Mendel in crossing pure tall peas with pure dwarf peas and their behaviour in subsequent generations.

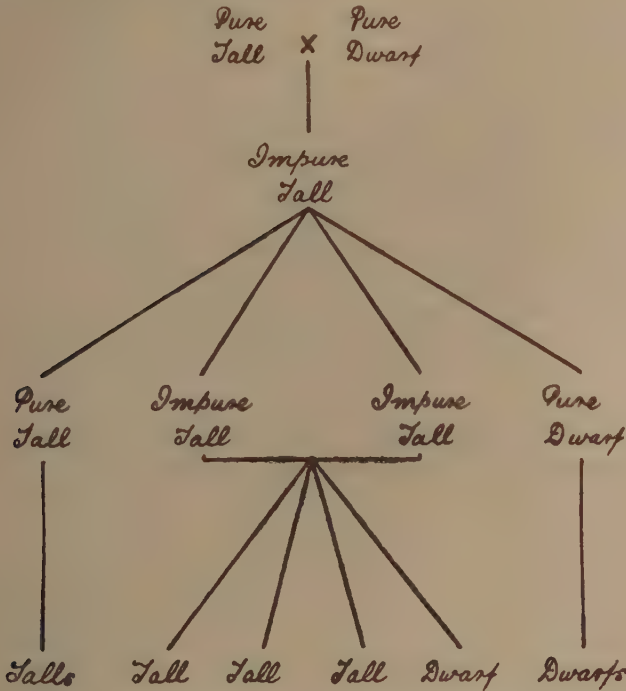


FIG. 116. SHOWING THE RESULTS OBTAINED BY MENDEL IN CROSSING TALL AND DWARF PEAS.

MENDEL'S LAW OF SEGREGATION.

Mendel's law of heredity was based on the experimental facts noted above. In order to give a reasonable explanation of such facts, Mendel conceived the idea of the separation or segregation of characters in the germ-cells. Mendel supposed, as Darwin and his successors have done, that each heritable character is represented in the germ-cells (both egg-cells and pollen-cells) by a certain determiner or factor. In the particular case we have been considering, the heritable characters are apparently tallness and dwarfness. Each individual plant raised from

fertilised seed is the product of its two parents, consequently it is a double structure determined by the coming together of the paternal and maternal factors.

A pure-bred tall pea, for instance, may be said to be the outcome of the meeting of a paternal factor for tallness with a maternal factor for tallness. Similarly, a pure-bred dwarf pea may be regarded as the consequence of the meeting of a paternal factor for dwarfness with a maternal factor for dwarfness. On the other hand, a cross-bred between a pure-bred tall pea and a pure-bred dwarf pea may be regarded as due to the meeting of the paternal factor for tallness with the maternal factor for dwarfness, or vice versa. Mendel's conception was that when the cross-bred formed its germ-cells (egg-cells and pollen-cells), the factors for tallness and dwarfness separated, the tall factor going into one germ-cell and the dwarf factor into another. In that case the germ-cells of the cross-bred would be of two kinds, and on the average one-half of them would be carrying the tall factor and one-half of them would be carrying the dwarf factor. Consequently, when the cross-bred was self-fertilised four distinct results would happen, on the average with equal frequency:

- (1) A pollen-cell carrying the tall factor might meet an egg-cell containing the tall factor, giving rise to a pure tall plant.
- (2) A pollen-cell carrying the tall factor might meet an egg-cell containing the dwarf factor, giving rise to an impure tall plant.
- (3) A pollen-cell carrying the dwarf factor might meet an egg-cell containing the tall factor, giving rise to an impure tall plant.
- (4) A pollen-cell carrying the dwarf factor might meet an egg-cell containing the dwarf factor, giving rise to a pure dwarf plant.

The diagram (fig. 117) on p. 303 will serve to illustrate Mendel's conception of germinal segregation. The tall plants are represented by oblongs and the dwarf plants by squares. The germ-cells of each plant are shown as circles. The contained tall factors appear black and the dwarf factors white.

If the diagram is compared with the previous one, it will be seen that Mendel's conception of germinal segregation fully explains the results obtained in his experiments. In further confirmation of the above interpretation of his results, Mendel made all the possible matings between the three germinal types. As we have already seen (fig. 116), both the extracted pure types bred true, while the impure type selfed gave all three types again. Mendel also mated the impure tall with the pure tall, and these gave, on the average, equal numbers

of impure tall and pure tall. He also mated the impure tall with the pure dwarfs, and these gave, on the average, equal numbers of impure tall and pure dwarfs.

The diagram (fig. 118) on p. 304 will illustrate these matings and their results, and at the same time Mendelian segregation in pure breeding,

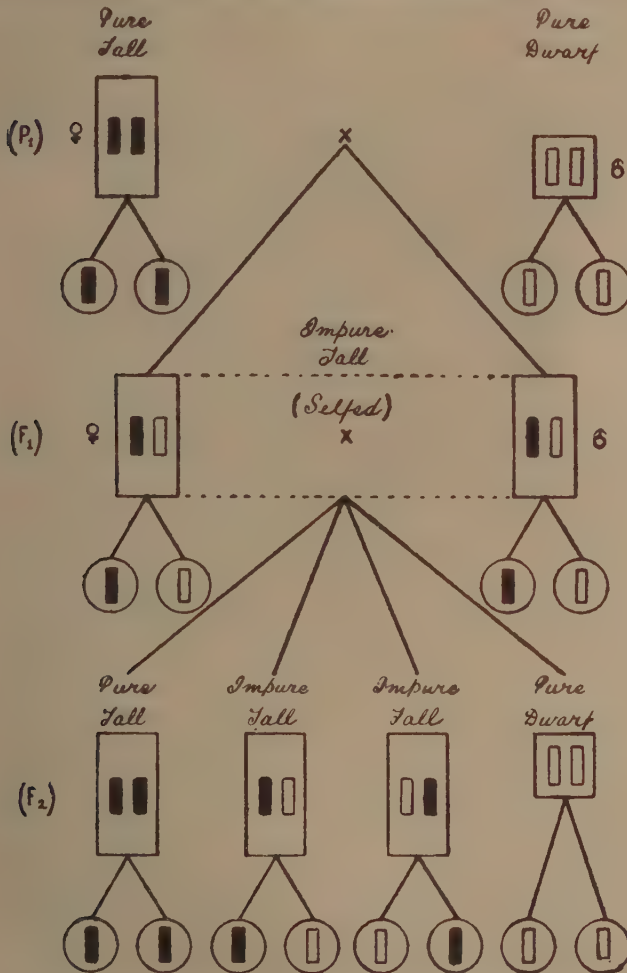


FIG. 117. ILLUSTRATING MENDEL'S CONCEPTION OF THE GERMINAL SEGREGATION OF THE FACTORS FOR "TALLNESS" AND "DWARFNESS" IN PEAS. (ALSO ILLUSTRATING THE "PRESENCE AND ABSENCE" METHOD.)

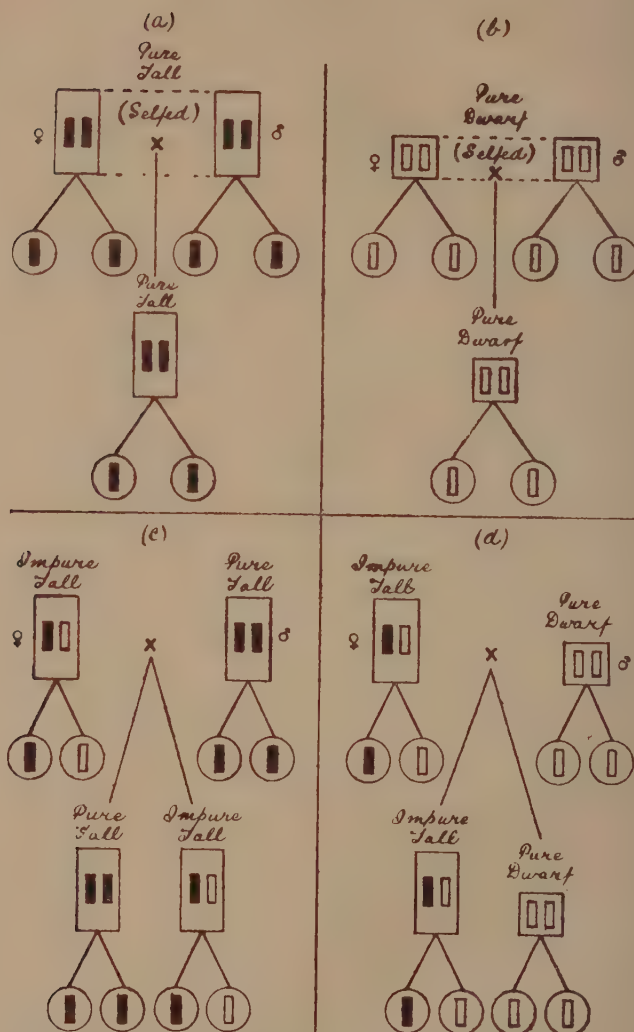


FIG. 118. FURTHER ILLUSTRATING MENDELIAN SEGREGATION.
(ALSO "PRESENCE" AND "ABSENCE.")

THE "PRESENCE AND ABSENCE" METHOD.

Recent experiments with many different characters in various plants and animals fully confirm Mendel's results with peas, and show clearly that Mendel's law of heredity is capable of general application. At the same time these results have suggested a more simple method of presentation of the facts of Mendelian segregation, which not only explains later developments better, but puts a different construction on the important phenomenon of Mendelian dominance. It is curious to observe how this striking phenomenon of dominance has proved a stumbling-block to many in their comprehension of the Mendelian principles, and yet seemingly it was this phenomenon that enabled Mendel to discover his simple law of segregation.

There seems to be no doubt that Mendel himself regarded tallness and dwarfness, for instance, as a definite pair of contrasting characters, which behaved in breeding as "dominant" and "recessive," and Mendel seems to have imagined that the definite germinal factors of each contrasting character actually segregated from one another in the reproductive cells. In view of recent experiments, however, we prefer to regard it more simply. In common with Mendel we regard tallness, for instance, as due to a definite germinal factor *present* in the tall pea, but on the other hand we regard dwarfness as simply due to the *absence* of the tall factor from the dwarf pea.

Thus in the *presence* of the tall factor the pea is tall, while in its *absence* the pea is dwarf.

Tallness appears to be dominant simply because it is present, and in its absence the seemingly recessive character is manifested. We prefer, therefore, to regard "presence" and "absence" of tallness as the two contrasting characters, rather than tallness and dwarfness. At first sight this may appear to be a distinction without a difference. But in reality the difference is important and promises to lead to far-reaching consequences, for it means that each heritable factor is a unit that may be distinct in its inheritance from all other factors. It is simply in its "presence" and "absence" that each heritable factor follows Mendel's law. The two diagrams above will also serve to illustrate the "presence and absence" method (figs. 117 and 118). In these the "presence" of the tall factor is marked by the presence of black in the spaces, while its "absence" is shown by the absence of black in the spaces, leaving them apparently white. It will be observed that in the pure tall there is a double presence of the tall factor made up of a single presence from

each parent, while in the impure talls there is only a single presence from one parent.

In other words, in the pure talls there is a double presence and in the impure talls a single presence, while in the pure dwarfs there is a complete absence of the tall factor.

In the same way we may take it that the presence of the factor for roundness prevents wrinkling and the pea is rounded, while in the absence of the round factor the pea is wrinkled. Similarly the presence of the factor for yellowness changes the green peas into yellow, while in its absence the peas remain green, and so on with other characters.

THE PHENOMENON OF "DOMINANCE."

The "presence and absence" method puts a different construction on the question of Mendelian "dominance." From the standpoint of "presence and absence" we cease to regard "dominance" as a particular mode of inheritance. We look upon it simply as due to the "presence" of a higher factor which somehow conceals the manifestation of a lower factor. Thus when we speak of a yellow pea as being "dominant" to a green pea we simply mean that the "presence" of the higher "yellow" factor conceals the manifestation of the lower "green" factor and the pea is yellow. On the other hand, in the "absence" of the higher "yellow" factor, the lower green factor, *present all the time in the yellow pea*, is manifested and the pea is green.

So far we have hardly any indications as to how the higher factors conceal the "presence" of the lower factors, but it seems likely that this phenomenon is part of the larger question of the interactions between the various unit factors in the production of visible characters. The complete solution of this important problem is for the future, and when it is fully solved, no doubt, we shall know more about heredity and variation. From the results of various experiments with plants and animals we already know that complete "dominance" is far from universal. In many cases the "dominance" is incomplete, the lower "recessive" character being manifested in various degrees in the cross-bred.

In such cases it would appear that a single presence of a unit-factor produces a different result from a double presence of the same factor. In other cases interaction between two unit-factors produces a new form distinct from both parents. It seems likely too, that the familiar blended and mosaic forms met with, especially in hybrids between

distinct species, are also due to the varied interactions between different unit-factors. All this goes to show that the phenomenon of Mendelian "dominance," though important, is but a secondary consideration quite distinct from Mendel's law of segregation.

In view of the adoption of the "presence and absence" method, which in the circumstances seems inevitable, the question naturally arises whether it is quite expedient to retain for general use the Mendelian terms "dominant" and "recessive." If these terms are applied in the original sense, as they usually are, to the "dominance" of a higher unit-factor over a lower unit-factor, then from the standpoint of "presence and absence" the application is unsound. While, on the other hand, if the terms are more properly restricted to the "presence" and "absence" of a single unit-factor it is to be feared that considerable confusion must arise.

On the whole, therefore, it would seem better to use the terms "higher" and "lower" ("epistatic" and "hypostatic" of Bateson) in place of "dominant" and "recessive," where two unit-factors are concerned.

APPLICATION OF MENDEL'S LAW TO HORTICULTURE.

Recent experiments have shown that many simple characters in garden plants follow Mendel's law. When the unit-factors happen to correspond with the horticultural characters, it is a simple matter for the breeder to breed quickly what he wants; for he knows that, according to Mendel's law, the plant manifesting the *lower* factor will breed true at once, and that by breeding from several individuals manifesting the *higher* factor one will be found which breeds true. This enables the breeder to dispense entirely with the old and laborious method of so-called "fixing" by continuous selection, which method, though usually effective in the end, is now clearly recognised as a waste of time.

Mendel's law provides a much quicker and more effective method of achieving the same result. Mendel's method was simply to *breed from single individuals separately*. By so doing the breeder can select the particular individual which breeds true in accordance with his requirements and increase his stock solely from that source. In that way the grower secures at once a true and permanent stock, which can be maintained simply by isolation.

BREEDING NOVELTIES BY RE-COMBINATION.

The combination of two pairs of simple characters by crossing, and the results which follow the self-fertilisation of such crosses, are of great utility to the breeder, for in the process of re-combination following Mendelian segregation new forms arise which will breed true in accordance with Mendel's law. Thus, Mendel himself crossed a round yellow with a wrinkled green pea, and obtained in the second generation two new forms—round green and wrinkled yellow peas, some of which bred true at once in accordance with his law.

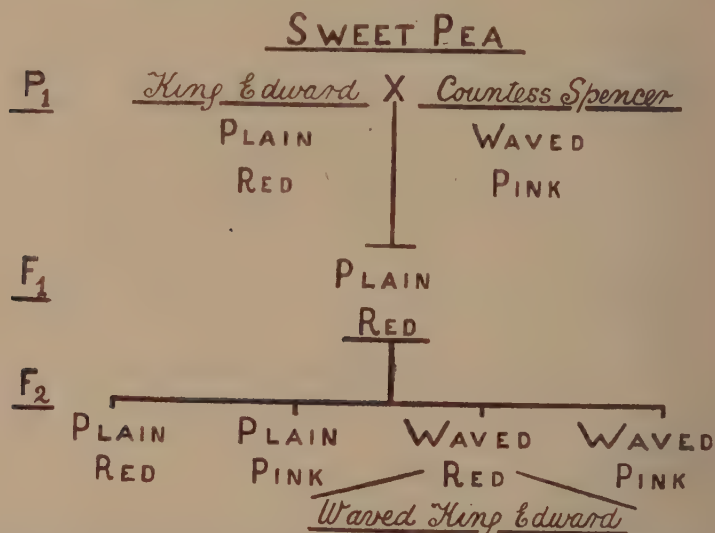


FIG. 119. SHOWING THE ORIGIN OF THE 'WAVED KING EDWARD' SWEET PEA BY RE-COMBINATION FOLLOWING MENDELIAN SEGREGATION.

By following Mendel's law Mr W. Cuthbertson, the well-known grower of sweet peas, states that he obtained in the *second* generation a true stock of the new and valuable variety, 'Waved King Edward,' by simply crossing the plain red 'King Edward' with the waved pink 'Countess Spencer'. The diagram (fig. 119) will illustrate how this was done. The plain red variety, 'King Edward,' crossed with the waved pink variety, 'Countess Spencer,' produced in the first generation (F₁) a plain red cross-bred, the lower waved and pink characters not

¹ *Sweet Pea Annual*, 1909.

being manifested, owing to the presence of the higher plain and red factors¹.

In the second generation (F_2) the plain red cross-bred self-fertilised produced four forms—plain red, plain pink, waved red, and waved pink—in accordance with Mendel's law.

Mr Cuthbertson did not apparently count the numbers of each type, but there should have been on the average nine plain reds, three plain pinks, three waved reds, and one waved pink. That is to say, out of every sixteen plants raised, three plants of the novelty 'Waved King Edward' would be the Mendelian expectation. On the average, one of these would breed true, while two would throw waved pinks again. By selecting the pure individual Mr Cuthbertson would thus secure a pure strain of the novelty in the second generation.

Mr Cuthbertson states that he raised the novelty 'Primrose Spencer' in a similar manner.

In my own experiments a few years ago I raised a true stock of 'Black Knight Cupid' in the second generation by crossing the ordinary tall 'Black Knight' with 'Pink Cupid.' In this case, however, three pairs of characters were concerned in the cross, and consequently, on the average, only three plants out of sixty-four were expected to be 'Black Knight Cupid,' and only one of these should breed true.

The actual numbers were as follows:

In the first experiment, out of 244 plants there were ten 'Black Knight Cupids,' the Mendelian expectation nearest in whole numbers being eleven. In the second experiment, out of 166 plants there were seven 'Black Knight Cupids,' the expectation being eight. In the third experiment, out of 165 plants there were only three 'Black Knight Cupids' instead of the expected eight².

Adding the results of the three experiments together, there were out of 575 plants twenty 'Black Knight Cupids,' where twenty-seven was the Mendelian expectation³.

¹ From a few results that I have seen it seems likely that when the 'Waved' or 'Spencer' type of sweet pea (now so popular with sweet-pea fanciers) comes to be critically studied in its Mendelian relationship to the "plain" and "hooded" types some complications will be found. Indeed, it would not be surprising to find that there are at least two genetic types of the 'Waved' sweet pea.

² In this experiment there were ten 'Cupids' which somehow failed to flower, owing probably to their being overcrowded.

³ In these experiments there was throughout a fairly uniform excess of tall, purples, light wings, and long pollens, with a corresponding deficiency of Cupids, reds, dark wings, and round pollens, the cause of which is at present obscure. On

310 *Origin of Black Knight Cupid Sweet Pea*

In the next generation (F_3) as expected some of the 'Black Knight Cupids' bred quite true, while others did not. Curiously enough, one plant gave a mixture of 'Black Knight Cupids' and *Wild Purple Talls*, which was probably due to the intervention of bees.

The following diagram (fig. 120) will illustrate the above experiment:

T, P, and L are higher factors; while C, R, and D are the corresponding lower factors.

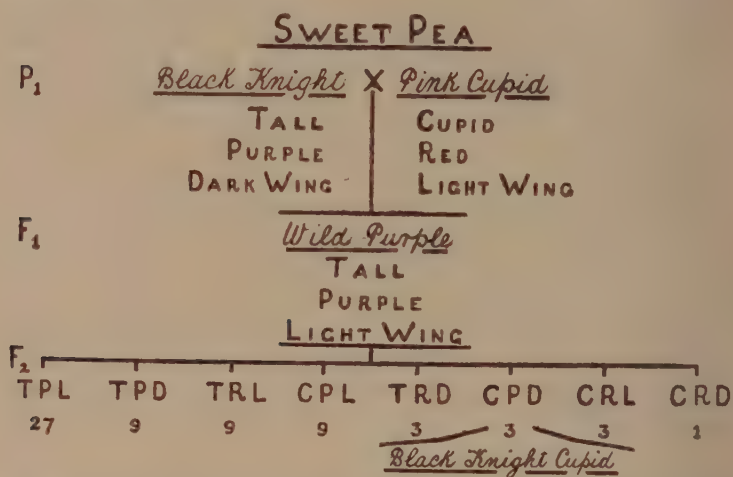


FIG. 120. SHOWING THE ORIGIN OF THE 'BLACK KNIGHT CUPID' SWEET PEA BY RE-COMBINATION FOLLOWING MENDELIAN SEGREGATION.

T=tall ; C=Cupid ; P=purple ; R=red ; L=light wing ; D=dark wing.

COMPOUND CHARACTERS.

In many cases, however, the unit-factors do not happen to correspond with the horticultural characters, and interesting complications then arise. For instance, in my experiments with tomatoes, red and yellow fruits behaved as units, red being the higher and yellow the lower; the presence of the "red" factor gave a red tomato, while in the absence of the "red" factor the tomato was yellow. But when the fiery red variety, 'Fireball,' was crossed with the pale-yellow variety, 'Golden Queen,' four distinct colour varieties appeared in the second generation (F_2). There were two kinds of reds and two kinds of yellows. This I

the whole the numbers were nearer 4 : 1 than the expected 3 : 1. There was also a partial coupling of purple colour with long pollen and red colour with round pollen but all the other characters were inherited independently.

found to be due to the fact that the fiery-red colour of 'Fireball' was really a compound of two unit-factors, representing red flesh and yellow skin, while 'Golden Queen' had yellow flesh and white skin. Consequently in the second generation two new varieties arose by re-combination—a carmine or "pink" tomato with red flesh and white skin, and a deep yellow tomato with yellow flesh and yellow skin. In accordance with the Mendelian expectation, a few individuals of these two new varieties bred true, while others did not (fig. 95).

The following diagram (fig. 121) will illustrate the results obtained in this experiment:

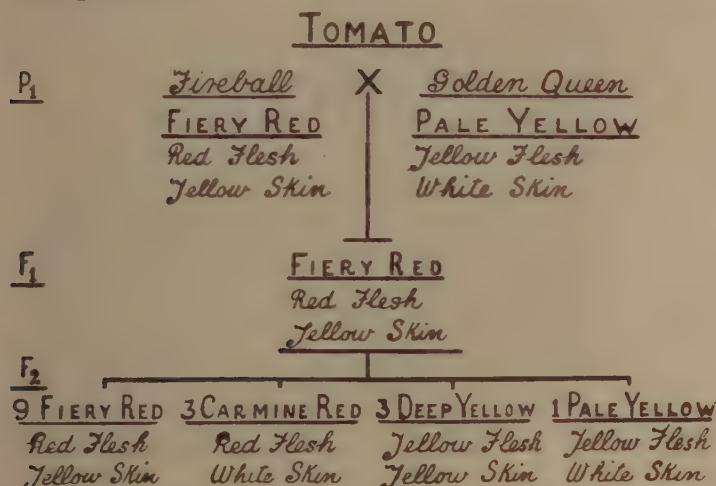


FIG. 121. SHOWING THE COMPOUND NATURE OF THE RED FRUIT OF THE 'FIREBALL' TOMATO AND THE APPEARANCE OF TWO NEW FORMS BY RE-COMBINATION FOLLOWING MENDELIAN SEGREGATION.

It will be observed that red flesh and yellow skin are both represented by higher factors appearing in F₁, while yellow flesh and white skin are represented by lower factors which are not manifested in F₁, owing to the presence of the higher factors for red flesh and yellow skin.

The Mendelian expectation of the four forms in the second generation was, of course, 9 : 3 : 3 : 1. The actual numbers observed were 31 : 11 : 10 : 3.

Similarly, Professor Bateson, by crossing a red sweet pea with a cream-coloured one, obtained *whites* in the second generation, the whites arising from the re-combination of the colourless plastids of the

red sweet pea with the colourless sap of the cream sweet pea. The following diagram (fig. 122) will illustrate the results obtained by Professor Bateson in his experiment:

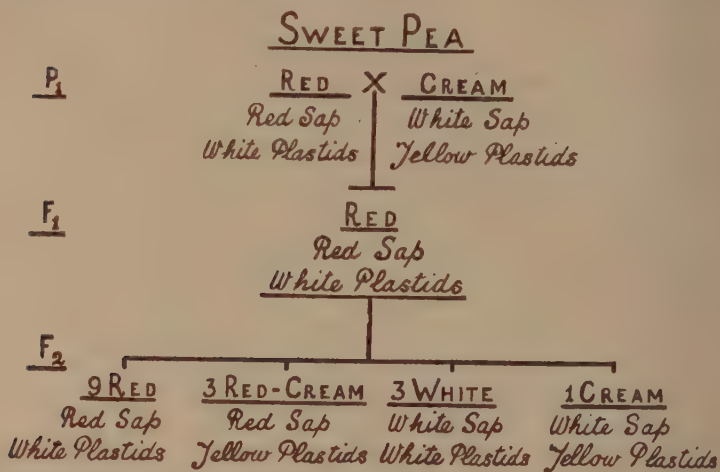


FIG. 122. SHOWING THE ORIGIN OF A WHITE SWEET PEA BY CROSSING A RED WITH A CREAM. RE-COMBINATION FOLLOWING MENDELIAN SEGREGATION. (After BATESON, SAUNDERS, and PUNNETT.)

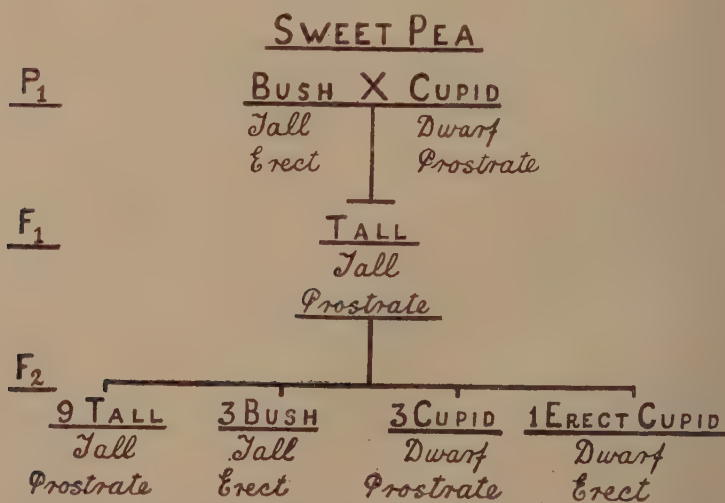


FIG. 123. ILLUSTRATING THE COMPOUND NATURE OF TALL, BUSH, AND CUPID FORMS OF SWEET PEAS. (After BATESON, SAUNDERS, and PUNNETT.)

An even more interesting result of the same nature has been obtained by Professor Bateson and Mr R. C. Punnett by crossing the Bush and Cupid forms of sweet peas.

In the first generation (F_1) all the cross-breds were, curiously enough, tall in habit like the ordinary sweet pea. In the second generation (F_2), however, there arose in Mendelian proportions tall, bush, ordinary prostrate Cupid and a new variety called 'Erect Cupid' with a peculiar habit of growth something like box-edging. This result has been shown to be due to the compound nature of these horticultural characters, the crossing of which leads to various recombinations in accordance with Mendel's law. The diagram (fig. 123) on page 312 will illustrate Professor Bateson's experiment and demonstrates the true nature of the tall, bush, and Cupid forms of the sweet pea.

Professor Bateson, Mr R. C. Punnett, and Miss Saunders have also found that the red colour of sweet peas and ten-week stocks is a compound character due to the presence of two unit-factors, in the absence of one of which the flower is white or cream. They also found that purple colour in sweet peas and stocks is due to the presence of a third unit-factor which only becomes patent in the presence of the other two. From this discovery follows the interesting fact that "albino" sweet peas and stocks (white or cream) may carry certain sap-colour factors which may become patent when the "albino" is crossed with another "albino" or with a coloured form. Other experiments show that various species of plants behave in a similar way.

For instance, Professor Bateson and Mr R. P. Gregory crossed *Primula sinensis* 'Crimson King' with *Primula sinensis stellata* 'Primrose Queen' (an "albino" form, white with large yellow eye). In the second generation (F_2) this cross gave crimson, magenta, rose, tinged white, and pure white forms: each colour appeared with small-eyes and large-eyes. All these appeared in "*sinensis*" and "*stellata*" forms, there being at least eighteen distinct forms, some of which bred true in accordance with Mendel's law.

In my own experiments I obtained similar colours by crossing crimson and white forms of the ordinary *P. sinensis*.

In another of my *Primula* crosses—palm-leaved "*stellata*" with red stems and pink flowers, crossed with fern-leaved "*sinensis*" with green stems and white flowers, I obtained in the second generation (F_2) 36 distinct forms, of which 34 were new in the sense that they were distinct from the original parents. Of these 34 I found that 14 could be bred true, while the remaining 20 were unfixable, being Mendelian hybrids.

PRACTICAL VALUE OF UNIT-FACTORS.

In view of the fact that a decade has hardly passed since the re-discovery of Mendel's long-lost paper, the progress made in Mendelian studies is indeed remarkable. Thanks mainly to the genius of Professor Bateson and the untiring labours of his co-workers at Cambridge, Mendelian analyses of garden plants have rapidly extended our knowledge of unit-factors. Equipped with such knowledge the practical breeder will be able to make new combinations with a certainty undreamed of ten years ago, and more important still, the breeder, by the use of Mendel's law, will be able to produce his novelties ready "fixed" without loss of time, and by strict isolation will be able to maintain a true stock without the trouble of "rogueing." It is impossible to refer in detail to the considerable work that has already been done in discovering unit-factors in garden plants by many experimenters. The numerous experiments with peas, beans, sweet peas, ten-week stocks, snapdragons, primroses, and other plants, by Mendel, Bateson, Punnett, Saunders, Correns, Tschermak, Johannsen, Lock, Biffen, Wheldale, Gregory, Shull, Emerson, Baur, and others are now well known¹. These valuable pioneer contributions are however but a beginning, and when we survey the vast extent of the field still unexplored, we realise that a huge harvest of results remains to be reaped by future experimenters. The unit-factors of such valuable garden plants, for instance, as orchids, roses, rhododendrons, chrysanthemums, dahlias, begonias, cinerarias, carnations, pansies, petunias, poppies, clematis, iris, gladiolus, lilies, geraniums, fuchsias, gloxinias, etc., are as yet practically unknown, to say nothing of the more difficult but equally important garden fruits, such as apples, pears, plums, cherries, gooseberries, currants, and strawberries. So far no garden plant can be said to have been thoroughly worked out by Mendelian analysis, but in a few cases great progress has been made, and for the practical guidance of breeders we may refer in some detail to two cases, the snapdragon and the sweet pea, which will serve as an illustration of the practical value of unit-factors. We will take the case of the snapdragon first, as the factors so far only refer to the flower colours.

¹ For references and details see Professor Bateson's *Mendel's Principles of Heredity*. Camb. Univ. Press, 1909.

UNIT-FACTORS IN THE SNAPDRAGON (*Antirrhinum majus*).

For the elucidation of the complicated colours of the modern snapdragon we are indebted to the exhaustive experiments of Miss Wheldale at Cambridge. No less than sixteen thousand plants have been raised and flowered in the course of these experiments. So far, Miss Wheldale has found at least seven unit-factors which go to make up the flower-colours of the snapdragon. All these factors are evidently present in the original wild form, which has self-coloured flowers of a "magenta" hue. Five of these factors may be represented as follows¹:

- Y** representing yellow colour in the lips.
- I** representing ivory colour in the lips.
- L** representing magenta tingeing in the lips.
- T** representing magenta tingeing in the tube.
- D** representing intensification of the magenta colour in the lips and tube.

The presence and absence of these five factors in various combinations and in their varied relations and interactions have given rise to the numerous colour-forms of the modern snapdragon, now so familiar in gardens. The following table will illustrate this so far as the five factors are concerned:

FACTORIAL TABLE FOR FLOWER COLOURS IN THE SNAPDRAGON
(*Antirrhinum majus*).

YILTD	Self-coloured magenta lips and tube (e.g. <i>wild form</i> , <i>Carmine King</i>).
YILT	Ivory lips and tinged with magenta.
YILD	Magenta lips and ivory tube (e.g. <i>Delila</i>).
YITD	Ivory lips and tube.
YLTD	Crimson lips and magenta tube (e.g. <i>Crimson King</i>).
ILTD	Pure white.
YIL	Ivory lips tinged with magenta, and ivory tube.
YIT	Ivory lips and tube.
YID	" "

¹ The remaining two factors are S representing a striped or streaked condition of the intensified magenta, and another factor representing a carmine pink pigment, which is present in the newer varieties of snapdragon known in gardens as 'Rose Doré.' The precise properties of these two factors are not yet fully known, so that for the present they may be omitted. Miss Wheldale states that the S factor behaves as a recessive to the D factor. It would appear therefore that the striping is due to the absence of a factor for uniform colour (say U) and that in the wild form this factor U is present together with D.

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YLT	Yellow lips and ivory tube tinged with magenta.
YLD	Crimson lips and ivory tube.
YTD	Yellow lips and ivory tube (e.g. <i>Yellow Prince</i>).
ILT	Pure white.
ILD	" "
ITD	" "
LTD	" "
YI	Ivory lips and tube.
YL	Yellow lips tinged with crimson, and ivory tube.
YT	Yellow lips and ivory tube (e.g. <i>Yellow Prince</i>).
YD	" " " " "
IL	Pure white.
IT	" "
ID	" "
LT	" "
LD	" "
TD	" "
Y	Yellow lips and ivory tube (e.g. <i>Yellow Prince</i>).
I	Pure white.
L	" "
T	" "
D	" "

All absent Pure white.

It will be observed that the various relations and interactions between the five factors in the case of the snapdragon are particularly interesting and suggestive. The factors I, L, T, and D can only be manifested in the presence of Y. In the absence of Y the flowers are pure white, while in the presence of Y all are coloured. I with Y gives "ivory." L with Y gives "crimson," but with I in addition it gives "magenta." T and D can only be manifested in the presence of L.

In order to show the simple effects of the presence and absence of the five factors and their somewhat complicated relations and interactions only a single presence of each factor is shown in the table. In accordance with Mendel's law, however, it will be quite understood that a pure-bred form would have a double presence of each factor; thus the pure-breeding wild form would be constituted YYIILLTTDD and so on with the others. Miss Wheldale found that the single presence of these five factors gave the same visible result as the double presence,

except that the single presence of L gave a lighter shade of "magenta" than the double presence.

The breeding results from the single presence and the double presence would, of course, be quite different. All the above combinations of factors may occur with either a double presence or a single presence of each factor in various combinations, in accordance with Mendel's law.

In the course of her experiments Miss Wheldale has incidentally cleared up certain difficulties in regard to the form known in gardens as 'White Queen.' This form has apparently *pure white* lips and tube, with a yellow palate. Nevertheless, Miss Wheldale's experiments demonstrate conclusively that in breeding it behaves precisely as if it were an *ivory*, the yellow form extracted from it in the second generation being rather paler in shade than the ordinary yellow¹.

UNIT-FACTORS IN THE SWEET PEA (*Lathyrus odoratus*).

The sweet pea has been specially investigated by Professor Bateson, Miss Saunders, and Mr Punnett. So far at least twelve unit-factors have been found which determine the habit of growth, flower form, and colour. All these factors are evidently present in the typical wild sweet pea, which has a tall and prostrate habit, with dark leaf axils; the flowers have an erect purple standard, with blue wings, the anthers are fertile, and the pollen grains are long.

Eight of these factors may be represented as follows:

- | | | |
|----------|--|-----------------------------|
| T | representing tallness of growth. | |
| P | representing prostrate habit of growth. | |
| W | representing whiteness in the flower. | |
| C | representing first sap-colour factor. | } Red colour in the flower. |
| R | representing second sap-colour factor. | |
| B | representing blue sap-colour in the flower. | |
| D | representing intensification of sap-colour in the flower. | |
| L | representing reduction of sap-colour in the wings of the flower. | |

The presence and absence of these eight factors in various combinations and in their varied relations and interactions have given rise to numerous types and colour forms, most of which are familiar in gardens.

The following table will illustrate this so far as the eight factors are

¹ Cf. *Report of Int. Conf. of Genetics*, 1906, p. 117 (see p. 253).

concerned¹. Other garden forms not found in the table are no doubt due to the presence of other unit factors not yet isolated.

FACTORIAL TABLE FOR HABIT AND FLOWER COLOUR IN THE
SWEET PEA (*Lathyrus odoratus*).

TPWCRBDL	Tall, purple standard with blue wings (e.g. <i>wild form, Purple Invincible</i>).
TPWCRBD	Tall, purple standard with purple wings (e.g. <i>Black Knight</i>).
TPWCRBL	Tall, white tinged with purple (e.g. <i>Lottie Eckford</i>).
TPWCRDL	Tall, red standard with blush wings (e.g. <i>Painted Lady</i>).
TPWCBDL	Tall, pure white (e.g. <i>Dorothy Eckford</i>).
TPWRBDL	" " "
TPCRBDL	Tall, purple cream standard with blue cream wings.
TWCRBDL	Bush, purple standard with blue wings.
PWCRBDL	Cupid, purple standard with blue wings (e.g. <i>Captain of the Blues Cupid</i>).
TPWCRB	Tall, white tinged with purple (e.g. <i>Lottie Eckford</i>).
TPWCRD	Tall, red standard with red wings (e.g. <i>King Edward</i>).
TPWCRL	Tall, white tinged with red (e.g. <i>Lovely</i>).
TPWCB	Tall, pure white (e.g. <i>Dorothy Eckford</i>).
TPWCBL	" " "
TPWCDL	" " "
TPWRBD	" " "
TPWRBL	" " "
TPWRDL	" " "
TPWB	" " "

¹ The remaining factors represent (1) dark leaf axil, (2) erect standard, (3) long pollen, (4) fertile anthers. The precise relationships between these remaining factors have not yet been fully worked out, but results so far have presented some interesting complications. For instance, a partial gametic coupling has been found (in coloured flowers) between the factors for dark axil and fertile anthers (pure white flowers have usually light axils). A partial gametic coupling also exists between the factors for long pollen and blue colour. Further a gametic repulsion between the factors for erect standard and blue colour has been discovered. There is also apparently a somatic coupling between erect standard and light wings and hooded standard and dark wings. In view of these complications these four factors may be for the present omitted.

TPCRBD	Tall, purple cream standard and wings.
TPCRBL	Tall, cream tinged with purple.
TPCRDL	Tall, red cream standard with blush cream wings (e.g. <i>Jeannie Gordon</i>).
TPCBDL	Tall, cream (e.g. <i>Hon. Mrs Kenyon</i>).
TPRBDL	" " "
TWCRBD	Bush, purple standard and wings.
TWCRBL	Bush, white tinged with purple.
TWCRDL	Bush, red standard with blush wings.
TWCBDL	Bush, pure white.
TWRBDL	" " "
TCRBDL	Bush, purple cream standard with blue cream wings.
PWCRBD	Cupid, purple standard and wings (e.g. <i>Black Knight Cupid</i>).
PWCRBL	Cupid, white tinged with purple.
PWCRDL	Cupid, red standard with blush wings (e.g. <i>Pink Cupid</i>).
PWCBDL	Cupid, pure white (e.g. <i>White Cupid</i>).
PWRBDL	" " "
PCRBDL	Cupid, cream standard with blue cream wings.
WCRBDL	Erect Cupid, purple standard with blue wings.
TPWCR	Tall, white tinged with red (e.g. <i>Lovely</i>).
TPWCB	Tall, pure white (e.g. <i>Dorothy Eckford</i>).
TPWCD	" " "
TPWCL	" " "
TPWRB	" " "
TPWRD	" " "
TPWRL	" " "
TPWBD	" " "
TPWBL	" " "
TPWDL	" " "
TPCRB	Tall, cream tinged with purple.
TPCRD	Tall, red cream standard and wings (e.g. <i>Queen Alexandra</i>).
TPCRL	Tall, cream tinged with red (e.g. <i>Evelyn Hemus</i>).
TPCBD	Tall, cream (e.g. <i>Hon. Mrs Kenyon</i>).
TPCBL	" " "
TPCDL	" " "
TPRBD	" " "

Factorial Table for Sweet Peas

TPRBL	Tall, cream (e.g. <i>Hon. Mrs Kenyon</i>).
TPRDL	" "
TPBDL	" "
TWCRB	Bush, white tinged with purple.
TWCRD	Bush, red standard and wings.
TWCRL	Bush, white tinged with red.
TWCB D	Bush, pure white.
TWCBL	" "
TWCDL	" "
TWRBD	" "
TWRBL	" "
TWRDL	" "
TWBDL	" "
TCRBD	Bush, purple cream standard and wings.
TCRBL	Bush, cream tinged with purple.
TCRDL	Bush, red cream standard with blush cream wings.
TCBDL	Bush, cream.
TRBDL	" "
PWCRB	Cupid, white tinged with purple.
PWCRD	Cupid, red standard and wings.
PWCRL	Cupid, white tinged with red (e.g. <i>Prima Donna Cupid</i>).
PWCB D	Cupid, pure white (e.g. <i>White Cupid</i>).
PWCBL	" "
PWCDL	" "
PWRBD	" "
PWRBL	" "
PWRDL	" "
PWBDL	" "
PCRBD	Cupid, purple cream standard and wings.
PCRBL	Cupid, cream tinged with purple.
PCRDL	Cupid, red cream standard with blush cream wings.
PCBDL	Cupid, cream (e.g. <i>Primrose Cupid</i>).
PRBDL	" "
WCRBD	Erect Cupid, purple standard and wings.
WCRBL	Erect Cupid, white tinged with purple.
WCRDL	Erect Cupid, red standard with blush wings.
WCBDL	Erect Cupid, pure white.
WRBDL	" "
CRBDL	Erect Cupid, purple cream standard with blue cream wings.

TPWC	Tall, pure white (e.g. <i>Dorothy Eckford</i>).	
TPWR	"	"
TPWB	"	"
TPWD	"	"
TPWL	"	"
TPCR	Tall, cream, tinged with red (e.g. <i>Evelyn Hemus</i>).	
TPCB	Tall, cream (e.g. <i>Hon. Mrs Kenyon</i>).	
TPCD	"	"
TPCL	"	"
TPRB	"	"
TPRD	"	"
TPRL	"	"
TPBD	"	"
TPBL	"	"
TPDL	"	"
TWCR	Bush, white tinged with red.	
TWCB	Bush, pure white.	
TWCD	"	"
TWCL	"	"
TWRB	"	"
TWRD	"	"
TWRL	"	"
TWBD	"	"
TWBL	"	"
TWDL	"	"
TCRB	Bush, cream tinged with purple.	
TCRD	Bush, red cream standard and wings.	
TCRL	Bush, cream tinged with red.	
TCBD	Bush cream.	
TCBL	"	"
TCDL	"	"
TRBD	"	"
TRBL	"	"
TRDL	"	"
TBDL	"	"
PWCR	Cupid, white tinged with red (e.g. <i>Prima Donna Cupid</i>).	
PWCB	Cupid, pure white (e.g. <i>White Cupid</i>).	
PWCD	"	"
PWCL	"	"
PWRB	"	"

PWRD	Cupid, pure white (e.g. <i>White Cupid</i>).
PWRL	" " "
PWBD	" " "
PWBL	" " "
PWDL	" " "
PCRB	Cupid, cream tinged with purple.
PCRD	Cupid, red cream standard and wings.
PCRL	Cupid, cream tinged with red (e.g. <i>Alice Eckford Cupid</i>).
PCBD	Cupid, cream (e.g. <i>Primrose Cupid</i>).
PCBL	" " "
PCDL	" " "
PRBD	" " "
PRBL	" " "
PRDL	" " "
PBDL	" " "
WCRB	Erect Cupid, white tinged with purple.
WCRD	Erect Cupid, red standard and wings.
WCRL	Erect Cupid, white tinged with red.
WCBD	Erect Cupid, pure white.
WCBL	" "
WCDL	" "
WRBD	" "
WRBL	" "
WRDL	" "
WBDL	" "
CRBD	Erect Cupid, purple cream standard and wings.
CRBL	Erect Cupid, cream tinged with purple.
CRDL	Erect Cupid, red cream standard with blush cream wings.
CBDL	Erect Cupid, cream.
RBDL	" "
TPW	Tall, pure white (e.g. <i>Dorothy Eckford</i>).
TPC	Tall, cream (e.g. <i>Hon. Mrs Kenyon</i>).
TPR	" " "
TPB	" " "
TPD	" " "
TPL	" " "
TWC	Bush, pure white.
TWR	" "
TWB	" "

TWD	Bush, pure white.
TWL	" "
TCR	Bush, cream tinged with red.
TCB	Bush, cream.
TCD	" "
TCL	" "
TRB	" "
TRD	" "
TRL	" "
TBD	" "
TBL	" "
TDL	" "
PWC	Cupid, pure white (e.g. <i>White Cupid</i>).
PWR	" " "
PWB	" " "
PWD	" " "
PWL	" " "
PCR	Cupid, cream tinged with red (e.g. <i>Alice Eckford Cupid</i>).
PCB	Cupid, cream (e.g. <i>Primrose Cupid</i>).
PCD	" " "
PCL	" " "
PRB	" " "
PRD	" " "
PRL	" " "
PBD	" " "
PBL	" " "
PDL	" " "
WCR	Erect Cupid, white tinged with red.
WCB	Erect Cupid, pure white.
WCD	" "
WCL	" "
WRB	" "
WRD	" "
WRL	" "
WBD	" "
WBL	" "
WDL	" "
CRB	Erect Cupid, cream tinged with purple.
CRD	Erect Cupid, red cream standard and wings.
CRL	Erect Cupid, cream tinged with red.

CBD	Erect Cupid, cream.
CBL	" "
CDL	" "
RBD	" "
RBL	" "
RDL	" "
BDL	" "
TP	Tall, cream (e.g. <i>Hon. Mrs Kenyon</i>).
TW	Bush, pure white.
TC	Bush, cream.
TR	" "
TB	" "
TD	" "
TL	" "
PW	Cupid, pure white (e.g. <i>White Cupid</i>).
PC	Cupid, cream (e.g. <i>Primrose Cupid</i>).
PR	" " "
PB	" " "
PD	" " "
PL	" " "
WC	Erect Cupid, pure white
WR	" "
WB	" "
WD	" "
WL	" "
CR	Erect Cupid, cream tinged with red.
CB	Erect Cupid, cream.
CD	" "
CL	" "
RB	" "
RD	" "
RL	" "
BD	" "
BL	" "
DL	" "
T	Bush, cream.
P	Cupid, cream (e.g. <i>Primrose Cupid</i>).
W	Erect Cupid, pure white.
C	Erect Cupid, cream.
R	" "

B	Erect Cupid, cream.
D	" "
L	" "
All absent	Erect Cupid, cream.

It will be observed that the various relations and interactions between the factors in the case of the sweet pea are quite different from those in the snapdragon.

Thus T with P gives the ordinary "Tall" habit, T alone gives "Bush" habit, P alone gives the ordinary "Cupid" habit, while absence of both T and P gives the form "Erect Cupid." Presence of W gives a pure white ground in the flowers, while absence of W gives a cream ground.

C with R gives red colour in the flower, while in the absence of either C or R the flowers are pure white or cream, according to the presence or absence respectively of W.

B is only manifested in the presence of both C and R giving purple colour.

D is only manifested in the presence of both C and R giving intensified colour.

L is only manifested in the presence of C, R, and D together, giving light-coloured wings.

As in the case of the snapdragon, only a single presence of the eight factors is given in the above table for the sake of simplicity. In accordance with Mendel's law it will, of course, be understood that a pure-bred form would have a double presence of each factor, thus the pure-breeding wild form would be constituted TTPPWCCRRBBDDLL and so on with the others. So far, however, the single presence of these eight factors apparently gives the same visible result as the double presence, but the breeding results would, of course, be quite different. All the above combinations of factors may occur with either a double or a single presence of each factor in various combinations in accordance with Mendel's law.

The results of these experiments with the snapdragon and the sweet pea show that the numerous and varied garden forms that have arisen from time to time under cultivation are simply due to the dropping out of certain unit factors.

It would appear, therefore, that the evolution of the snapdragon and the sweet pea under cultivation, so far from being an increase of complexity, as one might naturally assume, is in reality merely a simplification

of the original wild form. The philosophical significance of this fact cannot be dealt with here, but it is evident that the consequences of its application will be far-reaching indeed (cf. pp. 534—549).

The factorial tables of the snapdragon and the sweet pea given above will, it is hoped, assist breeders to arrange their matings so as to secure the results desired.

"ALBINO" ORCHIDS.

Recent results show that when true albino orchids (*i.e.* with no trace of purple sap colour) are crossed, the offspring may be all albinos, all coloured reversions, or both albino and coloured forms may be raised from the same capsule¹. For instance, *Paphiopedilum callosum* Sanderæ, (fig. 101) selfed by Mr N. Cookson, produced true albinos. Another batch, raised by Mr T. Statter, also produced true albinos. *P. Lawrenceanum* Hyeatum, selfed by Mr N. Cookson, produced nine plants, eight of which reproduced the true albino, while one plant is said to have reverted to an ordinary coloured form of *P. Lawrenceanum*. This apparent exception is remarkable, and a repetition of this experiment with larger numbers would be useful (fig. 58). *P. Lawrenceanum* Hyeatum \times *P. callosum* Sanderæ, raised by Messrs Charlesworth in 1900, produced the albino hybrid *P. \times Maudiae*, all the plants of which have so far proved to be true albinos. Another batch raised by Baron Schröder in 1907 also produced true albinos (fig. 102). *P. \times Maudiae* \times *P. insigne* Sanderianum (fig. 103), raised by Lieut.-Col. Holford in 1908, produced the albino hybrid *P. \times Rosettii*, sixteen plants of which have so far flowered, all apparently true albinos. It may be noted here that while *P. insigne* Sanderianum so far appears to behave as a true albino, yet the presence of some dark-coloured hairs at the base of the petals suggests that this variety may possibly be a tinged albino like *P. insigne* Sanderæ. It would be interesting to know if the hybrid *P. \times Rosettii* also has those dark-coloured hairs (fig. 104). *P. callosum* Sanderæ \times *P. bellatulum* album (fig. 105), raised by Mr Cookson in 1907, produced the coloured hybrid *P. \times Wottonii*, twenty-five plants of which have flowered, all apparently sap-coloured like the typical hybrid between *P. callosum* and *P. bellatulum*. *P. Lawrenceanum* Hyeatum \times *P. bellatulum* album, raised by Mr Cookson, produced the coloured hybrid *P. \times Lawrebel*, resembling the typical hybrid between *P. Lawrenceanum* and *P. bellatulum*. *Cattleya Mossiae* Wugeneri (fig. 106), selfed by Messrs Charlesworth in 1907, produced a true albino with no trace of sap

¹ For details see pp. 294—299.

colour. *C. Mossiæ Wageneri* × *C. Gaskelliana alba* (fig. 108), raised by M. Jules Hye, produced three true albinos—viz. *C. × Hyeæ*, *C. × Hyeæ Suzanne* (fig. 107), and *C. × Hyeæ Jungfrau*. *C. Mossiæ Wageneri* × *C. intermedia alba* (fig. 113), raised by Colonel Holford in 1906, produced the albino hybrid *C. × Mackayi Undine* (fig. 114), fourteen plants of which flowered true albinos. In 1908 three true albinos of the same parentage were raised by Mr R. G. Thwaites, also one by Sir Trevor Lawrence and one by Messrs Veitch. *C. Schröderæ alba* (fig. 112) × *C. intermedia alba*, raised by Mr Cookson, produced in 1907 the coloured hybrid *C. × Thayeriana*, similar to the hybrid raised by Mr Orpet between the typical *C. intermedia* and *C. Schröderæ alba*. *C. Gaskelliana alba* × *C. Harrisoniana alba* (fig. 110), exhibited by Mr Thwaites in 1908, produced the coloured hybrid *C. × Williamsiæ*, four plants of which had coloured flowers like the typical hybrid between *C. Gaskelliana* and *C. Harrisoniana*. *C. Gaskelliana alba* × *C. Warneri alba* (fig. 111), raised by M. Peeters in 1904, produced the hybrid *C. × Peetersiæ Myra* (fig. 109), five of which were true albinos with pure white flowers and green leaves, and two were coloured, having lilac-purple flowers with purple margins to the leaves.

These results are similar to those obtained in the Mendelian experiments of Professor Bateson, Mr R. C. Punnett, and Miss Saunders with sweet peas and stocks.

It is evident, therefore, that in orchids, as in sweet peas and stocks, the appearance of sap-colour depends on the simultaneous presence of two complementary colour factors, which may be termed C and R.

If both the colour factors C and R are present the sap is coloured; if either C or R is absent, the sap is colourless and the plant is an albino. Consequently different albinos may carry different colour factors; some may be C albinos, carrying the C factor, while others may be R albinos, carrying the R factor.

For instance, in the *Cypripedium* group results show that *Paphiopedilum callosum Sanderæ*, *P. Lawrenceanum Hyeæ*, *P. × Maudicæ*, and probably *P. insigne Sanderianum* and *P. × Rosettii*, may be regarded as R albinos, while, on the other hand, *P. bellatulum album* may be regarded as a C albino¹.

Similarly in the *Cattleya* group, for instance, *Cattleya Mossiæ Wageneri*, *C. Gaskelliana alba*, *C. × Hyeæ Suzanne*, *C. intermedia alba*, *C. × Hyeæ Jungfrau*, *C. × Mackayi Dusseldorffii*, *C. × Mackayi Undine*,

¹ It will of course be understood that C and R are purely arbitrary symbols which conveniently serve to distinguish the two colour factors from each other.

and *C. × Peetersiae Myra* may be regarded as R albinos, *C. × Peetersiae Myra* being an impure Rr, having only a single presence of R, the others being pure RR with a double presence of R. On the other hand, *C. Harrisoniana alba*, *C. Schraderæ alba*, *C. Warneri alba*, and probably *C. Mendelii alba* may be regarded as C albinos, *C. Warneri alba* being an impure Cc with only a single presence of C, the others being pure CC with a double presence of C.

To the orchid breeder who wishes to raise new and improved forms of valuable albinos by crossing, such knowledge is most useful. He will know, for instance, that all the R albinos will breed true albinos amongst themselves, whether selfed or crossed, and also that all the C albinos will breed true, selfed or crossed. On the other hand, he will know that if he crosses an R albino with a C albino he will get coloured reversions which, of course, he does not want. The orchid breeder will take care, therefore, to keep the C albinos distinct from the R albinos. This raises a question of great importance to the practical breeder. Mendel's law shows that individual albinos of the same species, to all outward appearance identical, may differ from one another in their germinal constitution and consequently give different results when bred from. It is, therefore, of prime importance for orchid breeders to adopt some simple method of identification for individual albinos, whether imported or raised from seed in gardens.

A distinct name would hardly be convenient for individuals which to the eye appear exactly alike, but identification might be assured by putting the name of the importer or raiser in brackets after the name of the albino, together with a number showing the order of its appearance. For instance, the albino *Paphiopedilum callosum Sanderæ* was first flowered from an importation of Messrs Sander in 1894, and this plant (and its many offshoots) might be called (Sander 1). Another individual of this albino appeared in an importation of Messrs Low in 1904, and might be called (Low 1), and so on.

The hand-raised seedlings of these albinos might be similarly distinguished, thus (Cookson 1), (Statter 1), and so on.

In this way all the individuals of any particular albino could be distinguished for stud purposes. The same principle might be adopted for special individual coloured forms, and indeed for garden plants generally, to the great advantage of breeders and growers. Standard stud individuals of known germinal constitution would then have a definite value, and their propagation and distribution would be more profitable to all concerned. Once the genetic properties of the in-

dividual plant are ascertained, all future breeding results from that plant (and its distributed offshoots) can be foreseen by the aid of Mendel's law.

MENDELISM AND THE SEED GROWER.

To none will the consequences of Mendelism appeal more strongly than to the professional seed grower. The prosperity—nay, the very existence—of his business depends on growing true stocks of seed. For centuries the seed grower has relied on "rogueing" to ensure a true crop. The process of "rogueing," however, though temporarily effective, involves in many cases a serious annual expenditure of trained and expensive labour, without permanently achieving its object. It is in this respect that Mendelism comes to the rescue of the modern seed grower. By the adoption of the Mendelian method of breeding from single individuals separately and selecting one only of those to perpetuate the true stock, the necessity for "rogueing" is practically dispensed with, and the true stock is permanently established without further selection, to the great advantage of the seed grower.

According to the old method a certain stock or strain was built up by the mass selection of several or many individual stock plants, and allowing them to breed together, the consequence being that some individuals breed true while others do not, and each strain or stock, even when carefully isolated, throws annually varying percentages of "rogues." The annual elimination of these "rogues" may or may not, according to chance, purify the strain in course of time.

The adoption of the Mendelian system of founding a true stock on a single individual may appear to be a simple matter, but in reality it is somewhat difficult to carry out in practice on a large scale, and extensive operations require a good deal of careful organisation to be truly effective. In order to ensure the final selection of a single true breeding individual, many single individuals have to be selected. Each one of these must be so disposed, that during the flowering season all are strictly isolated not only from one another but from anything else of a similar nature. The seeds of each individual must be separately harvested, stored, and tested in the trial grounds, and so on.

But once the true-breeding individual is found, its stock and seed will, with strict isolation, be permanently established, without any further selection or "rogueing," and can be increased annually to any extent.

It is obvious that apart altogether from the question of the recognition of the advantages of the Mendelian system of breeding, there are certain practical difficulties that have to be faced. In any extensive operations the initial expenses of carrying out the Mendelian system of breeding are bound to be heavy, and early returns are not to be expected. Later returns, however, should fully compensate the grower.

Old methods of cultivation die hard, and in the circumstances, it is not surprising that professional seed growers generally have hesitated to adopt the new methods, even in the few cases where they clearly recognise the great advantages of the Mendelian system. Once a beginning has been made, however, there will be no looking back, for there is no doubt that the Mendelian system of breeding has come to stay.

Mendelism stands or falls by the purity of its cultures. No other method of plant-breeding is known which can guarantee 100 per cent. of purity in its cultures. When buyers once realise that such a cherished dream is practicable there will be no more "rogues," and Mendelian seeds will be the only profitable seeds to grow.

XXIV

MENDELISM AND SEX¹

The question of the determination of sex is an old one. It is a problem which has been much debated along various lines of inquiry. Until recently it not only eluded all solution, but gave no promise of solution.

Recent Mendelian experiments, commenced about the year 1900, had not, however, been very long in operation before the conclusions to which they led afforded clear suggestions that the problem of sex could be investigated by the same methods and with the aid of the same directing principles. Mendelism, in fact, has provided the key by which the question can be accurately and experimentally answered. Much, however, remains to be done, for the knowledge which we now possess is to be regarded as in the nature of a right beginning rather than as a final solution.

Until quite recently it was generally believed that external conditions determined the sex of individuals. It was assumed that if we knew these conditions we should be able to decide at will the sex of the unborn young. Acting under the influence of such a belief, several investigators designed and carried into operation various experiments that were intended to show the part which different factors in the environment played in the determination of sex. The well-known experiment of Yung with tadpoles was of this class. In this experiment, certain tadpoles were fed on very nutritive and abundant food, while others were fed on less nutritive and limited material. It was found that there was a larger percentage of female frogs derived from the former and of male frogs from the latter. The conclusion thus suggested itself that females were determined by excessive anabolic or building up process of nutrition, and males by that antithetic process in which anabolism only just keeps in excess of the katabolic or breaking down processes. But there were several sources of error in such an experiment. The most serious one is indicated by a similar experiment with the caterpillars of certain butterflies. In this experiment it was ascertained that under-feeding

¹ An address delivered to the Mendel Society, London, March 29th, 1909, at the invitation of Mrs Haig-Thomas.

did not result in the production of an excess of males, but in the elimination of the females. There being a heavy mortality among the females, it is a natural consequence that there appears to be an excess of males. But it is apparent and not real. It is, therefore, in reality, not a case of sex-determination by environmental influences, but one of survival of the fittest. The males are more resistant to the harsh effects of a low nutritive diet than are the females. Moreover, the interesting case of the bee should have been sufficient to expose the fallacy of the belief that the environment can determine sex. The queen bee lives under special and uniform conditions, and she is fed on highly nutritive material. If conditions determine sex, then she should produce offspring definitely predominating in one direction with respect to sex, for it should be mainly feminine or mainly masculine. Moreover, if high nutrition determined the formation of females, then the parthenogenetic eggs of the unfertilised, but specially fed, queen bee should be mainly or wholly female. But the reverse is the case. The unfertilised eggs all produce male bees or drones, while females or workers are alone produced from the fertilised eggs. The simple fact that the act of fertilisation thus determined the sex of the individuals arising from fertilised eggs is by itself sufficient to show that sex is determined within the germ-cells, and is not dependent on environment.

It is recognised now, by those who are engaged in the experimental investigation of the question of sex and of cognate problems, that sex itself, like other qualities, is predestined in the germ-cells, and is definitely determined by fertilisation. And, when it has thus been predestined and determined, external influences cannot alter it. It is, however, possible that in particular cases the proportions in which the sexes may appear are determined by environmental influences. In the case of the butterfly caterpillars mentioned above, certain conditions associated with semi-starvation, while they do not determine sex itself, do determine the proportion of males and females, by unduly eliminating the latter without influencing the former. But this difference in the resisting powers of the two sexes is probably exceptional, and, as a rule, the sexes are similar in their inherent responsive powers towards special environmental conditions.

In the majority of cases, where we are in possession of sufficiently accurate statistics, it appears that as a general fact the sexes are produced in equal numbers. This is so for Man, for the lower animals, and for unisexual plants. The production of the two sexes in equal numbers is a significant fact from the Mendelian standpoint. It had no

meaning whatever in pre-Mendelian days; but now its interpretation is clear. The individual distinctness of the sexes is also a significant fact. It indicates the complete segregation of maleness and femaleness. This segregation of the sexes and their occurrence in equal numbers at once suggested the well-known Mendelian ratio of 1 : 1. This ratio is the result of mating a Mendelian hybrid with an individual carrying the recessive character, and it indicates that one of the two sexes is a dominant to the other. If we use the symbols which have been previously described, and if we tentatively regard the female as a dominant hybrid and the male as a pure recessive, or *vice versa*, then they will be respectively symbolised as DR and RR . A reference to the table of matings shows that the expected offspring from a DR parent mated with an RR one, will consist in equal numbers of DR 's, which in this case will be females—if we regard the female character as dominant—and of RR 's, which will be males. Thus far, then, the two general facts already known to us, namely, the segregation and numerical equality of the sexes, strongly suggest that sex is predestined in the germ-cells and is hereditarily transmitted in accordance with the Mendelian principles of gametic purity and segregation.

It was not, however, until quite recently that experiments specifically designed to answer the questions presented by sex have, by their results, extended the suggestion into proof. Among the most important and interesting of such experiments we must place those of Professor Correns with two species of the Bryony plant. In the species known as *Bryonia dioica* female flowers are found on one plant and male flowers on another; the two sexes are borne on different individuals, so that any particular plant is either male or female, and not hermaphrodite like the majority of plants. The other species, named *Bryonia alba*, has the sexes borne on different flowers but on the same plant. Each individual plant is therefore hermaphrodite, bearing both male flowers and female flowers. When the flowers of a female *B. dioica* are crossed with those of a male *B. dioica*, the offspring consist of a mixture of male and female plants.

The most interesting crosses, however, are the reciprocals between the hermaphrodite plant of the *B. alba* and the two unisexual plants of *B. dioica*. When the flowers of the female plant of *B. dioica* are crossed with the male flowers of *B. alba*, all the individuals in the offspring are female plants¹. But the reciprocal cross, strangely enough, gives a very

¹ A few exceptions—2 males with 589 females—are said to occur, and a few of the females bear occasional male flowers.

different result; for, when the female flowers of *B. alba* are pollinated with pollen from the flowers of a male *B. dioica*, the offspring consist of male and female plants in approximately equal numbers.

Correns endeavoured to interpret these results in the following way. Let us take first the cross of male *B. dioica* with female *B. dioica*. The result, as we have seen, is a mixture of males and females in equal numbers. We will for the moment assume, as Correns did, that maleness is dominant; that the male plants are Mendelian hybrids and therefore carry two kinds of pollen-cells in approximately equal numbers, one-half bearing the character of maleness and the other half that of femaleness; and that the female plant, being recessive, must be pure with regard to femaleness, and all its egg-cells will therefore carry femaleness alone. It is clear that a cross of the nature which we are now considering will resolve itself into the simple Mendelian one of DR by RR . The DR here represents the male plant and the RR the female plant. The symbol D in this case stands for maleness, which is dominant, and R for femaleness, which is recessive. Since the female plant bears only "female" egg-cells and the male plant bears both "male" and "female" pollen-cells in equal numbers, it must happen in the random meetings resulting from pollination that one-half of the "female" egg-cells will be fertilised with "male" pollen-cells which will give us DR offspring, and one-half with "female" pollen-cells which will give us RR offspring. Therefore, since maleness is dominant, the individuals which result from a fertilisation of R egg-cells by D pollen-cells will be hybrids and will be visibly male. Thus there will be produced equal numbers of hybrid males (DR 's) and of pure females (RR 's). So far, then, the Mendelian interpretation is in accordance with the experimental facts, and it gives them an intelligible unity.

Let us pass next to consider the crosses between the two different species. As we have already seen, they resolve themselves into crosses of the two following kinds:

NATURE OF CROSS.		
BRYONIA DIOICA (Unisexual)	× BRYONIA ALBA (Hermaphrodite)	RESULT OFFSPRING
(1) Flowers of female plant	× Male flowers	= All females
(2) " " male	" × Female flowers	= Males and females

Now, as we have already pointed out, the individuals of *Bryonia alba* are hermaphrodite, bearing both male and female flowers. In other words, as individuals they are not differentiated with regard to sex.

We here meet with a new kind of cross, different from that between the unisexual individuals of *B. dioica*. When the unisexual individuals of this latter species are crossed with each other, we are really dealing with the crosses of two differentiated individuals, in each of which the one sex has segregated from the other. But in the cross of *B. dioica* with *B. alba* we are dealing with one where a sexually differentiated individual is crossed with an undifferentiated one. The results show that we may regard differentiation and non-differentiation (absence of differentiation) as definite characters capable of hereditary transmission. Hence we are here dealing with a cross between a differentiated unisexual plant and a non-differentiated hermaphrodite one, the unisexual character being apparently dominant.

Let us first consider case No. 2 in the table above. Some of the pollen-cells of the male flower of *B. dioica* are carrying maleness and others are carrying femaleness. The egg-cells of the female flowers of *B. alba* are carrying undifferentiated hermaphroditism. In a cross of the kind we are considering, two results may happen. For both the male and female carrying pollen-cells of *B. dioica* will meet the egg-cells of *B. alba* carrying the hermaphroditic character. In the former case there will be produced fertilised egg-cells bearing the characters of maleness and hermaphroditism. These cells when they develop into individuals will produce unisexual males, because both unisexuality and maleness are dominant. The second possible result will be attained in the latter case, when fertilised cells having the composition of femaleness and hermaphroditism are formed. These cells will give rise upon development to unisexual female individuals, because unisexuality is dominant over hermaphroditism. Thus two kinds of individuals are expected on this interpretation, unisexual males and unisexual females. And the experimental results do, as we have seen, confirm this Mendelian expectation.

Now we will take the reciprocal cross as shown in case No. 1 in the table. Here again we meet with the undifferentiated hermaphroditism of *B. alba*, but now carried in its pollen-cells. In this cross, then, only one result, and not two, as in case No. 2, will occur: the egg-cells carrying femaleness alone of *B. dioica* will be fertilised by the pollen-cells of *B. alba*, which are carrying hermaphroditism alone; and since unisexuality is dominant to hermaphroditism, all individuals produced by this cross will manifest the unisexual female character. Hence, our Mendelian interpretation expects females only to result from such a cross, and experiment has shown that such is the case.

While the Mendelian interpretation devised by Correns does undoubtedly enable us to give an intelligible statement of the probable processes at work, it is not altogether free from objection. The assumption of the undifferentiated nature of both the pollen and egg-cells of *B. alba*, with the further necessary assumption that these have a composition different from those of *B. dioica*, is one that would require a great deal of evidence in its favour before we should be justified in finally accepting it.

But there is a simpler interpretation which quite as adequately fits the facts and does not involve the serious assumption necessitated by Correns' theory. It is the interpretation of Professor Bateson. In his scheme we regard not the male, but the female, as being dominant. The pollen-cells of *B. dioica* are regarded as homozygous carrying maleness alone, while the pollen-cells of *B. alba* are also regarded as homozygous but carrying femaleness alone. The female or egg-cells of both species are regarded as heterozygous. Individuals of both species will possess two kinds of egg-cells, and these will occur in approximately equal numbers. One-half of them will carry maleness and the other half femaleness. We shall then expect that when the egg-cells of *B. dioica* are fertilised with the pollen-cells of the same species, there will be produced equal numbers of male and female offspring; for when a pollen-cell which carries maleness meets an egg-cell which, as we have postulated, carries maleness alone, clearly the resulting offspring from such a fertilisation must be male; but when the second kind of egg-cell, that which carries femaleness, meets a pollen-cell carrying maleness, it is clear that if femaleness is dominant, the resulting offspring will be female. The male is pure maleness, while the female is a hybrid, carrying both maleness and femaleness.

Similarly, the offspring resulting from fertilising the egg-cells of *B. dioica* carrying either maleness or femaleness with the pollen-cells of *B. alba* carrying femaleness alone, are expected to consist of heterozygous (hybrid) females and homozygous (pure) females in equal numbers. That is, so far as visible characters are concerned—for we cannot distinguish these two kinds of females by inspection—the offspring are expected to consist entirely of females, and experiment shows that such is the case.

In the reciprocal cross of the egg-cells of *B. alba* carrying either femaleness or maleness fertilised with the pollen-cells of *B. dioica* carrying maleness alone, it is expected that one-half of the offspring will be heterozygous females and one-half homozygous males. And

again experiment confirms our expectations, in so far that the offspring does not consist of an equal number of males and females¹.

The application of Mendelian methods and interpretation to the consideration of the experimental results does, therefore, give us an intelligible and consistent statement of the ascertained facts. No previous theory has ever accomplished that; and we may, I think, feel assured that at last we are on the right road towards the elucidation of this difficult but interesting problem.

There are reasons for believing that the different factors which determine the hereditary characters of organisms are carried by certain nuclear bodies called the chromosomes. In form they are sometimes rod-shaped and sometimes horseshoe-shaped, and they make their appearance within the nucleus just before cell division is about to occur. They stain very darkly with certain dyes and their presence is thus rendered more manifest. For the individuals of a given species, the number of chromosomes present in the nuclei of the cells is constant. But the number of chromosomes in the body or somatic cells is, however, twice that in the germ-cells or gametes of any individual. Consequently, when at fertilisation two germ-cells, paternal and maternal, unite, the resulting cell, out of which a new individual will arise by cell division, contains the higher or somatic number of chromosomes. Thence during all the cell divisions which occur as the new individual develops from this fertilised cell, this higher or body number is retained in all the somatic cells which result. But, at a certain stage, the individual forms its germ-cells, and during the process the number of chromosomes becomes reduced to one-half.

Now there is clear evidence, derived from the study of these chromosomes in certain insects, phylloxerans, and aphids, to show that in some way sex is directly determined by, or its determination is correlated with, the presence of an accessory chromosome in certain of the paternal cells. That is, if the egg-cells contain five chromosomes then one-half of the sperm-cells or spermatozoa will also contain five, but the other half will contain four only. There are thus two kinds of spermatozoa developed. We owe this interesting observation to the investigations of Professor Wilson, Professor Morgan, and Miss Stevens. Between them they have examined about a hundred species of insects and other animals, and in all of them they have found these two forms of spermatozoa present.

¹ It would be interesting to know whether *B. alba* when self-fertilised produces female plants as well as hermaphrodites, as it should do according to this scheme.

Now it is very clear that if there are two kinds of spermatozoa in certain animals, the one kind approximately equal in number to the other, and there exists only one kind of egg-cell, in random fertilisations one-half of the eggs will be fertilised by one kind of spermatozoa and the other half by the other kind. And from the fertilised eggs, fertilised by two different kinds of spermatozoa, it is to be expected that there

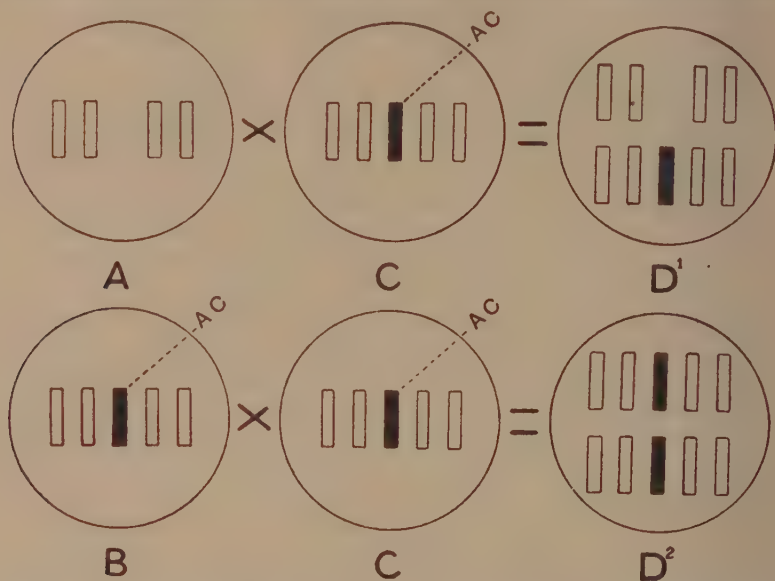


FIG. 124. Diagram (after Wilson) to illustrate the difference in the somatic composition of the male (D^1) and the female (D^2) zygotes or individuals in the insect *Anasa*. In *Anasa* there is one kind of egg-cell (C), but two kinds of spermatozoa (A and B). Male individuals (D^1) result from the union of a paternal germ-cell (A), which is devoid of an accessory chromosome with a maternal germ-cell (C), which contains one (AC). Female individuals (D^2) result from the union of a paternal (B) and maternal germ-cell (C), both of which contain an accessory chromosome (AC).

The male individual (D^1) thus contains one chromosome less than the female (D^2). will arise two kinds of individuals. Let us illustrate this by reference to the above diagram (Fig. 124). In this diagram A represents the spermatozoon carrying only four chromosomes, while B represents the other form of spermatozoon, that which carries five chromosomes. We may speak of the fifth or odd chromosome as the accessory one. The egg-cells are all of one type and carry five chromosomes; they are represented in the diagram by C. Now when A and C unite it is clear

that the zygote or fertilised cell D^1 will contain only nine chromosomes, or one less than the zygote D^2 . This latter, which is formed when B and C unite, contains ten chromosomes. The former zygote will be a male, for the observations of the three investigators just mentioned have shown that the somatic or body cells of the males investigated by them contain one chromosome less than the body cells of the females. The latter zygote will be a female, since it contains the full complement of chromosomes.

If these observations prove to be of general application, then it would appear that sex is determined by the presence or absence of the paired condition of the accessory chromosome. If it is paired in the zygote, femaleness results; if it is unpaired, then maleness results. But, whether the zygote shall contain the paired or unpaired accessory chromosome depends upon the kind of spermatozoon by which fertilisation is effected. The male is the arbiter which decides the result.

These interesting discoveries in connection with the chromosomes of cells enable us to frame explanations of several things which were previously incapable of any satisfactory or consistent statement. We may therefore next turn our attention to the new interpretation of old facts which these discoveries enable us to frame.

As is well known, the eggs laid by the queen bee are some of them fertilised and some not; but both sorts of eggs develop. The unfertilised ones, however, give rise to the male drones, while the fertilised eggs produce the workers, which are immature or imperfect females. In order to understand this result we must first consider another fact in connection with the chromosomes of germ-cells. We have already seen that in certain insects there are two kinds of sperm-cells or spermatozoa; one of these carries an accessory chromosome and its union with the egg-cell produces a female, while the other kind is devoid of the accessory chromosome and the egg fertilised by it develops into a male. Now, if we suppose that something happened by which all the latter kind of sperm-cells became destroyed, it is obvious that male offspring would never be produced. The product of fertilisation would be females always, and this we know is the case, not only with the fertilised eggs of the bee, but also of the green-fly (*Aphis*), of a water-flea (*Daphnia*), and of a certain genus of plant-lice (*Phylloxera*). Is there then any evidence that this seemingly improbable selective destruction of a particular type of sperm-cell does actually occur? Such a hypothesis appears to be exceedingly fanciful. None the less, it expresses an actual fact which has been ascertained by careful observation. For

Professor Morgan has observed that in a *Phylloxera* one-half of the sperm-cells are small in size and do not contain the accessory chromosome, and ultimately degenerate: they therefore can take no part in fertilisation. But these are the cells which determine maleness in the offspring which arise from the eggs fertilised by them. Therefore, fertilisation being effected only by the other kind of cell, females alone are produced. Miss Stevens has observed a similar condition of degeneration of those sperm-cells which are devoid of the accessory chromosome in another genus of plant-lice, *Aphis*. And in bees the degeneration of one-half of the sperm-cells has also been observed by Meves.

In this way our knowledge of the behaviour of the accessory chromosome, while rendering it certain that sex is a gametic differentiation, that it is a quality not depending upon environmental influences, also enables us to explain the phenomenon that in bees, plant-lice, and water-fleas, fertilised eggs develop only into females. For femaleness, as has been shown by Professor E. B. Wilson in the insect *Protenor*, and by Professor Morgan in certain species of *Phylloxera*, is characterised by the presence in the body cells of the full complement of chromosomes, while maleness is characterised by the absence of one or two of these.

It may therefore be accepted as a demonstrated fact that in certain insects and in certain phylloxerans and aphids the body cells of the females possess one—or in some cases two—chromosomes more than those of the male. It is also a fact that in some insects, phylloxerans, and aphids there are two kinds of spermatozoa, one kind, which is smaller than the other, containing one or two chromosomes less than the larger kind. The smaller ones, which are the carriers of maleness, degenerate, and leave, therefore, only the larger ones, which are carriers of femaleness, to effect fertilisation. It therefore follows as a natural sequence that from fertilised eggs only females are produced.

These being the facts with regard to insects, phylloxerans, and aphids, and, further, it being known as an observed fact that in the bee one-half of the spermatozoa undergo degeneration, we may be justified in believing that the same explanation is applicable there. We may feel fairly certain that when the case of the bee has been adequately investigated we shall find that the reason why all its fertilised eggs produce females only is because the male-bearing spermatozoa are the ones which degenerate.

We pass next to consider why it is that in the bee the unfertilised

eggs—that is, the virgin or parthenogenetic eggs—always give rise to drones, which are male individuals. Here again we must seek our interpretation by appealing to facts which have been ascertained in phylloxerans and aphids. We have already seen that Professor Wilson and Professor Morgan have observed in certain insects (Wilson) and in phylloxerans and aphids (Morgan) a certain difference in the number of chromosomes in the body cells of the females and males. In the males of insects and aphids and in some phylloxerans there is one chromosome less than in females; but in other phylloxerans there are two less. Morgan has quite recently shown that there are two kinds of parthenogenetic eggs, one containing a pair of accessory chromosomes and the other not; that is, one kind contains two more chromosomes than the other kind. Moreover, he has shown that in *Phylloxera fallax* this internal difference is correlated with a difference in size, the egg which contains the accessory pair of chromosomes being larger than the one without; and he has further observed that the large parthenogenetic egg produces females while the small one gives rise to males. Now this difference between the two kinds of eggs arises in the course of maturation, for previous to this they both contain the higher number of chromosomes. At the formation of the polar body, twelve chromosomes remain in the large egg, and only ten in the small one. It is clear then, that in the former case there has been no extrusion of the pair of accessory chromosomes during the formation of the polar body, while in the latter case they have been extruded into the polar cell. In other phylloxera and in aphids only one and not two chromosomes is thus extruded.

We thus see that those parthenogenetic eggs which are destined to give rise to males have one or more chromosomes eliminated from them. We may suppose this is also the explanation why the parthenogenetic eggs of the bee produce males alone. They apparently are all of one kind, and have had their accessory chromosome extruded during their maturation. They therefore carry the reduced number of chromosomes characteristic of the male somatic tissues.

The next case of sex-inheritance we may consider is that which results when the currant moth (*Abraxas grossulariata*) is crossed with its lighter coloured variety *lacticolor*. Before the series of experiments which we are about to describe were made by Mr Doncaster, *lacticolor* was known to occur only in the female form, for males were unrecorded. When *lacticolor* female is crossed with *grossulariata* male, the offspring consist of the *grossulariata* form alone, there being males and females

in approximately equal numbers. It is clear from this result that *lacticolor* is recessive, since it does not appear in the F_1 generation. With regard to the dominance of one sex or the other, we may for simplicity regard the female as being dominant and as carrying maleness recessive, as we did for *Bryonia* (*supra* p. 336). The appearance of both males and females in the F_1 generation is then quite consistent with that assumption. Let us now see how the other possible crosses fall into line with such a scheme.

If this representation is right, then the F_1 *grossulariata* males will be all $G L \text{♂}$ ¹ and all the females will be $G L \text{♀}$. The *grossulariata* character being dominant, both these forms are visibly *grossulariata*, but the male character being recessive can only manifest itself when femaleness is absent; hence the first form is a pure male and the second is visibly female, but carries male recessive. It is necessary before we go farther to make another working assumption. It is, however, not only adequately supported by the facts of these particular experiments, but by other experiments in sweet peas. The assumption which the experimental facts compel us to make is, that between the *grossulariata* character and femaleness there is repulsion, as a consequence of which the two are never carried in the same germ-cell.

Let us summarise the position before going farther. The *grossulariata* character is dominant over the *lacticolor* one; femaleness is dominant and carries maleness recessive, and as a correlative outcome of this maleness is therefore recessive and pure; between the *grossulariata* character and femaleness there exists repulsion. Accepting these premises, we expect, on the basis of Mendelian principles, the following results when the crosses indicated below are made:

Visible Nature of Cross	Visible Character of Offspring
$L \text{♀} \times G \text{♂}$	$= G \text{♀} + G \text{♂}$
$G (\overset{*}{L}) \text{♀} \times G (L) \text{♂}$	$= G \text{♀} + G \text{♂} + L \text{♀}$
$L \text{♀} \times G (L) \text{♂}$	$= G \text{♀} + G \text{♂} + L \text{♀} + L \text{♂}$
$L \text{♂} \times G (L) \text{♀}$	$= G \text{♂} + L \text{♀}$

* It should be borne in mind that the *lacticolor* character is not manifested when *grossulariata* is also present, and the recessiveness of the former is indicated here by enclosing it in brackets. It should also be remembered that all females are carrying maleness recessive and therefore not manifesting it.

¹ Where G =*grossulariata*, L =*lacticolor*, ♂ =male and ♀ =female.

Now these expectations are fulfilled by the experimental results, for the above table is but an epitomised statement of them, as well as being a tabulated expression of Mendelian predictions.

For the information of those who desire a full statement of the zygotic and gametic composition of the parents, and the zygotic composition of the offspring, the following table is appended. The four crosses here represented are the same as those given in the table above, and they are placed in the same relative order.

Zygotic Composition of Parents	Gametic Composition of Parents	Zygotic Composition of Offspring
$\begin{array}{c} LL \text{♀} \delta \\ \times \\ GG \delta \delta \end{array}$	$\begin{array}{c} L \text{♀} + L \delta \\ G \delta \end{array}$	$\left\{ \begin{array}{l} = GL \text{♀} \delta + GL \delta \delta \\ \quad G \text{♀} \quad G \delta \dagger \end{array} \right.$
$\begin{array}{c} GL^* \text{♀} \delta \\ \times \\ GL \delta \delta \end{array}$	$\begin{array}{c} G^* \delta + L \text{♀} \\ G \delta + L \delta \end{array}$	$\left\{ \begin{array}{l} = GG \delta \delta + GL \delta \delta + \\ \quad GL \text{♀} \delta + LL \text{♀} \delta \\ \quad \quad G \text{♀} \quad \quad L \text{♀} \end{array} \right.$
$\begin{array}{c} LL \text{♀} \delta \\ \times \\ GL \delta \delta \end{array}$	$\begin{array}{c} L \text{♀} + L \delta \\ G \delta + L \delta \end{array}$	$\left\{ \begin{array}{l} = GL \text{♀} \delta + GL \delta \delta + \\ \quad \quad G \text{♀} \quad \quad G \delta \\ \quad LL \text{♀} \delta + LL \delta \delta \\ \quad \quad L \text{♀} \quad \quad L \delta \end{array} \right.$
$\begin{array}{c} GL^* \text{♀} \delta \\ \times \\ LL \delta \delta \end{array}$	$\begin{array}{c} G^* \delta + L \text{♀} \\ L \delta \end{array}$	$\left\{ \begin{array}{l} = GL \delta \delta + LL \text{♀} \delta \\ \quad \quad G \delta \quad \quad L \text{♀} \end{array} \right.$

* It is one of the working hypotheses that this individual in forming its germ-cells cannot carry the *grossulariata* character and femaleness in the same germ-cell or gamete, since these two characters are assumed to repel each other. But they can of course be carried in the same individual or zygote.

† The symbols in smaller type represent the *visible* character of the offspring. Those in larger type represent their estimated composition.

The scheme by means of which we have thus endeavoured to give a consistent statement of the seemingly remarkable and apparently incoherent experimental facts is one which we owe to Professor Bateson and Mr R. C. Punnett.

One feature of a general but very important nature remains to be considered. The *grossulariata* individuals used in the experiments were taken wild. And in the cross of the male of this with the female *lacticolor* variety, all the offspring, as we have seen, were *grossulariata*. This fact indicates that the wild male *grossulariata* is pure with regard

to that character; but quite recently, Doncaster has made the reciprocal cross, namely, wild female *grossulariata* with certain male *lacticolors* bred in the course of the experiments. The offspring consists of males *grossulariata* and females *lacticolor*. As Professor Bateson points out¹ this is a striking result, and is not only a confirmation of the validity of his scheme of interpretation, which was framed before this fact was known, but it leads to a most important and far-reaching conclusion. Because clearly it means that the wild female *grossulariata* moths living in districts where the *lacticolor* variety is unknown, are in reality hybrids of *lacticolor*, carrying that character recessive. The males, as we have seen, are pure *grossulariata*. For hundreds of generations, possibly, the *lacticolor* variety has been in existence, hidden recessive in the females of the wild *grossulariata*; it has not been manifested because the males are pure and the *grossulariata* character is dominant. Some light is thus thrown upon the nature and origin of variations. We may be justified in believing that the *lacticolor* variety became a manifest one by a germinal change in one or more of the eggs of a wild female *grossulariata*, resulting in the elimination of the factor which produces the larger spotted condition that chiefly distinguishes *grossulariata* from its variety *lacticolor*.

The first individuals, like the later ones of the variety, would be all females, and these would necessarily have to cross with the wild male *grossulariata* in order to perpetuate their race.

Fundamentally similar to the sex-inheritance of the characters we have just considered in the currant moth, is that of the black-eye in the "green" or the yellow canaries and the pink-eye of the cinnamon canaries. Miss Durham has shown that the pink-eye condition of these latter birds applies only to the early days after hatching, for, as they grow older, pigment of a chocolate colour appears. Although the pigment in the eyes of adult cinnamon canaries is really chocolate, yet it appears to be black, owing to the degree of concentration in which it occurs. The pigment in the eyes of the "green" and yellow canaries is really, and not apparently, black.

The chief feature of general interest which is manifested by these experiments is of the same order as that we have just considered in the currant moth. Miss Durham's experiments seem to show that while the male black-eyed canary² is pure with regard to that character,

¹ *Mendel's Principles of Heredity*, Cambridge.

² It does not matter whether the black-eyed canary is a "green" or a yellow one. The result is the same.

the *female* is hybrid and carries the pink-eye (or, in reality, the cinnamon character)¹ recessive. It will be remembered (*supra* p. 344) that among moths the *male grossulariata* was similarly pure with regard to the *lacticolor* character, while the *female* was hybrid.

In canaries the existence of this remarkable condition is shown by the different nature of the offspring in the reciprocal crosses, for when male "black-eye" is crossed with female "pink-eye," all the offspring are black-eyed, both the males and the females: but when male "pink-eye" is crossed with female "black-eye," then among the offspring all the males are black-eyed and all the pink-eyed are females². The result is thus one which follows from a mating of the ordinary Mendelian kind, namely, $D R \times R$ giving 1 $D R$ + 1 $R R$. In this case the female black-eyed bird is the $D R$, and the pink-eyed male is the $R R$. The black colour of the eye is dominant = D , and the pink-eye, or absence of blackness, is the recessive = R .

The new fact which these experiments reveal is what in past days we should have called the correlation or coupling of the pink-eyed condition with femaleness, now we regard it not as a coupling of femaleness and pink-eyedness, but as a *gametic* repulsion existing between femaleness and black-eyedness. It is important to bear in mind that this repulsion exists in the gametes (germ-cells) only, and that the female is a dominant and a hybrid with regard to sex. That being so, hen birds may be black-eyed; but it must be remembered that while the zygote (the individual) manifests femaleness and black-eyedness, all its germ-cells which carry femaleness will only carry pink-eyedness. Its visible femaleness combined with black-eyedness is due to the fact that both these qualities, as well as maleness and pinkness, which are both recessive, were brought in at the fertilisation of the egg-cell from which it has developed.

We may tabulate these facts and their associated hypotheses as below.

Since the pink-eyed condition is really due to the absence of black pigment, we may regard the alternative factors as being blackness = B and absence of blackness = b . In such case, we should substitute the symbol b for that of P in the table following. Similarly we may regard (*infra* p. 346) maleness as simply a condition which is left when

¹ In addition to the eye characters the cinnamon further differs from the green canary in having light brown (cinnamon) markings instead of black ones. This colour is due to chocolate pigment.

² Four cases occurred in which the hens were black-eyed.

femaleness is withdrawn. In other words, maleness is simply absence of femaleness.

The two cases, namely, the currant moth and the canary, which we have last considered, are instances of what may be described as sex-linked inheritance: that is, a certain character in its inheritance is transmitted by the germ-cells which are carrying either maleness or femaleness, but not by both. There is thus conceivably a process of repulsion between this particular character and one of the sexes, when the factors which determine both are brought into association, in the ripening germ-cells. In both the cases we have just considered it is femaleness which exerts this repelling influence upon the particular character.

Zygotic Composition of Parents	Gametic Composition of Parents	Zygotic Composition of Offspring
$\begin{array}{c} PP \text{ } \text{♀} \text{ } \text{♂} \\ \times \\ BB \text{ } \text{♂} \text{ } \text{♂} \end{array}$	$\begin{array}{c} P \text{ } \text{♀} + P \text{ } \text{♂} \\ B \text{ } \text{♂} \end{array}$	$\left. \begin{array}{c} \\ \\ \end{array} \right\} = \begin{array}{cc} BP \text{ } \text{♀} \text{ } \text{♂} + BP \text{ } \text{♂} \text{ } \text{♂} \\ B \text{ } \text{♀} \qquad B \text{ } \text{♂} \dagger \end{array}$
$\begin{array}{c} PP \text{ } \text{♂} \text{ } \text{♂} \\ \times \\ BP \text{ } \text{♀} \text{ } \text{♂} \end{array}$	$\begin{array}{c} P \text{ } \text{♂} \\ B \text{ } \text{♂} + P \text{ } \text{♀} \end{array}$	$\left. \begin{array}{c} \\ \\ \end{array} \right\} = \begin{array}{cc} BP \text{ } \text{♂} \text{ } \text{♂} + PP \text{ } \text{♀} \text{ } \text{♂} \\ B \text{ } \text{♂} \qquad P \text{ } \text{♀} \end{array}$

† See second note, p. 343.

There is another case apparently similar which came under my notice in the course of some experiments with poultry. Certain recessive white fowls carry the hidden factor which, meeting colour, produces grey-white feathers barred with blue-black. This "barred" character is called by fanciers "cuckoo" colour. When recessive white hens carrying "cuckoo" are crossed with black cocks, the offspring consist simply of "cuckoo" cocks and black hens (see p. 232).

The facts of the experiments may be interpreted by assuming that the "cuckoo" factor is repelled by that for femaleness, so that the two can never occur in the same germ-cell. Hence all germ-cells which carry femaleness will be devoid of this barring-factor. The case, indeed, seems to be similar to those which we have already more fully discussed.

We pass on now to consider sex in Man. From the general fact which

has been obtained from statistics derived from various sources, that the number of males and females are approximately equal at birth, we may say that in Man, too, the inheritance of sex is probably Mendelian, and follows the scheme $DR \times RR$. We have no reliable evidence at present that enables us to say whether maleness or femaleness in Man is dominant¹.

Quite recently a book on Sex in Man, written by Dr Rumley Dawson, has appeared. It does not deal with the subject from the Mendelian standpoint—indeed, the author is apparently not acquainted with Mendelism. But he formulates a remarkable and striking hypothesis, in support of which he describes a number of interesting facts.

To put them briefly, the principal points in his theory are these: The male exercises no influence at all in the causation of sex; this influence is wholly exercised by the female. From various clinical data he arrives at the conclusion that the female produces both male and female ova. This conclusion is interesting, since it is one which is quite Mendelian, but is arrived at by different methods from those employed by the Mendelian, and by one who is not apparently acquainted with Mendelism. But the feature of greatest interest in his theory is his assumption that the right ovary produces male ova and the left ovary female ova. He then further supposes that only one ovary is active and ovulates each month, the other not discharging any eggs. They thus alternately ovulate every other month, so that one month the right ovary is discharging male ova and the next month the left ovary will discharge female ova.

From these premises he proceeds to show that in normal cases, if we know the sex and date of birth of the first child, the sex of the following children can be predicted for any particular month, and, therefore, a boy or a girl can be begotten at will. The author produces some good evidence in favour of his theory, but it cannot yet be regarded as fully tested.

He tests his theory by considering some of the Royal Families. If ovulation occurs every twenty-eight days, there will be thirteen periods of ovulation in each year. Consequently, in every succeeding twelfth month, the sex of the offspring will be the opposite

¹ In his recent studies on human spermatogenesis Professor T. S. Painter of the University of Texas finds that in both White Man and Negro there are 48 chromosomes (24 pairs) and that the Sex chromosomes are of the XY type as in *Drosophila* in which the male is dominant and heterozygous for Sex. (*Note added 1925.*)

of that in the first month. If in any October a baby girl was born, then if a birth should occur at the following October, the expectation is that it will be a boy. The author considered the date of the births of the children of various Royal personages. Taking Queen Victoria's family, we find that the Empress Frederick (Princess Victoria) was born in November, 1840, and King Edward VII in November, 1841. In the case of the Duke of Edinburgh's family, a son was born in October, 1874, and a daughter in October, 1875. With the Duke of Connaught's family, a daughter was born in January, 1882, and a son in January, 1883. The family of the Tsar of Russia is interesting, since there are five children. Princess Olga was born in November, 1895, Princess Tatiana in June, 1897, Princess Maria in June, 1899, Princess Anastasia in June, 1901, and Prince Alexis in August, 1904.

So far, these instances and many others might be quoted to support the theory, since prediction is fulfilled by fact. But Mr Mudge has recently sent me the case of an Irish family in which two out of five predictions are apparently falsified.

A theory must not be judged too severely upon the basis of a few exceptions. Ovulation may have been suspended or irregular, or other disturbing causes may temporarily have disturbed the normal sequence. And if a large number of families, taken at random, in general confirm the theory, the exceptions to it must be regarded as exceptional. But there are certain theoretical objections to the theory, into which we cannot now enter. Further it appears that the author's assumption, that the male does not influence the determination of sex, is inconsistent with a number of facts. For, as we have already seen (*supra* p. 339), in some cases the male is the arbiter of sex; and, in all cases by virtue of his definite gametic composition, he may be said to exercise as much influence as the female in the determination of the sex of his offspring. (See footnote p. 347.)

If we now briefly summarise the facts and conceptions which we have considered in detail, we may say the evidence is clear that sex is predestined in the germ-cells, and is determined at the moment of fertilisation. It is highly probable, too, that sex is due to a germinal factor, and there seems to be but little doubt that it is inherited in accordance with Mendel's law.

We have, however, to recognise the possibility that the females and the males of different organisms in the animal and vegetable kingdoms may be differently constituted. The evidence shows that in canaries, fowls, possibly in rabbits, and in some insects, the female is

apparently a Mendelian dominant hybrid, carrying the character of maleness as a recessive, while the male is a Mendelian recessive homozygote, and is therefore pure for maleness. On the other hand, in many insects, and possibly in lobsters and crabs, it is the male which is apparently the Mendelian dominant hybrid, carrying femaleness as a recessive.

The existence of these two types of sex leads us to suppose that in sex-heredity we have one more case in support of the "presence and absence" theory of Mendelian characters. In this newer scheme by which experimental results are symbolically represented, we still retain the original terms of dominant and recessive used by Mendel, but they are applied in a different way. When a pure grey rabbit is crossed with a black one, all the offspring are grey. Mendel would have spoken of the grey colour as being dominant to black which would be regarded as recessive. In other words, he would have looked upon the pair of alternative characters as being grey *versus* black. But we do not now so regard them. We believe the facts are better represented by constituting the alternative characters as presence of grey *versus* absence of grey which gives black¹. The presence of the character is thus dominant to its absence, so that presence of greyness is not said to be dominant to the presence of blackness, but to the absence of greyness. In the sense that the terms dominant and recessive are applied to the manifestation or non-manifestation in the zygote of the two unit-characters of an alternative pair, the terms are still used in the way in which Mendel employed them. But, as we have just seen, the conception of the nature of alternative characters has been modified. Dwarfness, for instance, is not now regarded as another quality to tallness, but simply as that condition which results from absence of tallness. Add the factor which determines tallness to dwarfness, and tallness is manifested. And similarly in respect to sex, we may conceive that femaleness is due to a germinal factor which determines the manifestation of that sex. It is something which is added to maleness, and in its absence maleness is manifested. The two alternative unit-characters of sex are therefore presence and absence of femaleness.

This conception of sex seems to be applicable to all cases which have yet been investigated, and it enables us to give a consistent interpretation of the facts in the two types of sex-inheritance which we have studied. Thus, if we let F represent femaleness and f its

¹ Grey being epistatic to black which is hypostatic.

absence, then, since the female seems to be a dominant hybrid, the female zygotic composition may be represented as Ff . But the male is pure with regard to maleness, and since this is simply absence of femaleness, the zygotic composition may be symbolically represented as ff .

With regard to the other type of sex-inheritance, that represented in certain insects where the male seems to be the dominant hybrid, we have already seen (compare Fig. 124) that the male somatic cells carry one chromosome less than the female. In other words, femaleness is due to the presence of a chromosome absent in the male. In both types of sex-inheritance, therefore, femaleness may be said to be due to the presence of an element absent in the male, as recently pointed out by Professor Castle, of Harvard University.

XXV

MENDELIAN CHARACTERS IN PLANTS, ANIMALS AND MAN¹

The year 1866 marks an epoch in the history of Evolution. In that year Mendel published in this journal his classical memoir on heredity. More than a quarter of a century elapsed ere Mendel's remarkable contribution attracted the attention of the scientific world, and in the meantime the great man passed away unknown to the world of science. The simultaneous discovery of Mendel's memoir by de Vries, Correns and Tschermak, early in the year 1900, is one of the romances of science.

Since 1900, Mendel's fame has increased by leaps and bounds until at the present moment the cult of Mendelism is spread far and wide over the civilised world. When one considers that the Mendelian principles of heredity were based on a few simple experiments with the common garden pea, this rapid development is indeed remarkable. The living power and truth of Mendelism can only be due to the fact that the experiments of Mendel, simple though they be, were conceived, completed, and interpreted by a master mind.

Mendel's great discovery was the *reality of segregation*. Other observers had noted the phenomenon of segregation in both plants and animals, but Mendel was the first to perceive its reality, and to realise its true meaning.

While others were content to regard segregation merely as irregular variation, Mendel perceived that segregation implied a regular mode of inheritance that was not only qualitative but quantitative, and the demonstration of the Mendelian ratios led naturally to Mendel's conception of differential characters.

In his experiments with garden peas Mendel found seven pairs of differential characters, viz.:—Rounded and wrinkled seeds, yellow and green cotyledons, coloured and white seed-coats, inflated and constricted seed-pods, distributed and bunched flowers, and tall and dwarf stems.

¹ Reprinted from "Festschrift zum Andenken an Gregor Mendel," XLIX. Band der *Verhandlungen des Naturforschenden Vereines in Brünn*, pp. 192—213 (1911).

Mendel demonstrated that all these differential characters truly segregated after crossing.

During the last few years, many experimenters, in many lands, have applied the Mendelian principles to many kinds of plants and animals, including Man himself. These experiments have yielded a heavy harvest of facts which fully confirm Mendel's original conceptions of the nature of heredity.

In illustration of this, a list of characters in plants, animals and Man, which have been found to be subject to Mendel's law of segregation, is given below, together with the names of the experimenters and observers concerned in their determination. This list, though fairly comprehensive, is by no means complete, and new characters are being added almost every day¹.

LIST OF CHARACTERS SUBJECT TO MENDEL'S LAW.

(a) PLANTS.

Agrostemma.

Purple, and pale coloured flowers. (de Vries.)

Amarantus.

Red, and green foliage. (de Vries.)

Anagallis.

Red, and blue flowers in the Pimpernel. (de Vries, and Tschermak.)

Antirrhinum.

Tall, short, and dwarf habit of growth in the Snapdragon.

Green, yellow, white, and variegated leaves.

Normal, and peloriate flowers.

Pure white (weiß), "White Queen," ivory (elfenbein), and yellow (gelb) flowers.

Pale (bläß), intermediate (mittel), and deep (dunkel) coloured forms of rose-doré (chamois-rosa auf elfenbein), bronze (chamois-rosa auf gelb), magenta (rot auf elfenbein), and crimson (rot auf gelb) flowers.

¹ In compiling this list of Mendelian characters no attempt has been made to detail the germinal factors concerned in the formation of the visible characters noted in the list. In certain cases, therefore, characters included may be merely different reactions of the same germinal factors, while others may be due to various combinations of unit-factors.

Tinged (fleischfarbig), self-coloured (ganz), Delila, striped (gestreifte) and marbled (picturatum) forms of each of the above 4 colours. (de Vries, Wheldale, Baur, and Hurst.)

Aquilegia.

Green, and variegated leaves in the Columbine. (Baur.)

Aster.

Coloured, and white flowers. (de Vries.)

Atropa.

Red, and green stems, brown, and yellow flowers, black, and yellow fruits in the Nightshade. (de Vries, Bateson, and E. R. Saunders.)

Avena.

Black, yellow, grey, and white glumes in Oats.

Presence and absence of ligules. (John Wilson, and Nilsson-Ehle.)

Berberis.

Hairy, smooth, 3 spined, and 5 spined stems, yellow, and orange flowers. Revolute, flat, glaucous, green, and purple leaves. (C. E. Saunders, and Hurst.)

Brassica.

White, and yellow flesh in Swedes and Turnips.

Bulbing, and non-bulbing stems.

Lacinate Kale, Swede, Kohl Rabi, and Cabbage foliage.

Green, and purple leaves. (Sutton, and Hurst.)

Bryonia.

Red, and black fruits, monœcious, and diœcious flowers, male and female sex. (Correns, Bateson, and E. R. Saunders.)

Bursa (Capsella).

Angular, and rounded capsules. *Heteris*, *tenuis*, *rhomboidea*, and *simplex* forms of *B. bursa-pastoris* and *B. Heegeri*. (Shull.)

Campanula.

Blue, and white flowers.

Normal, and monstrous calyx. (de Vries, and Correns.)

Canavalia.

Tall, and semi-dwarf habit of growth.

Pink, and white flowers.

Red, and white testa. (Lock.)

Cattleya.

Purple, and white (albino) flowers. (Hurst.)

Chelidonium.

Normal, and laciniate leaves and petals. (de Vries.)

Chrysanthemum.

Yellow, and white flowers. (de Vries.)

Clarkia.

Magenta-red, salmon-pink, and white flowers. (Bateson, Punnett, and de Vries.)

Coreopsis.

Yellow, and brown flowers. (de Vries.)

Cucurbita.

Size, and shape of fruits. (Emerson.)

Datura.

Red, and green stems.

Violet, and white flowers.

Prickly, and smooth fruits. (de Vries, Bateson, E. R. Saunders, and Baur.)

Delphinium.

Single, and semi-double flowers.

Blue, pink, and white flowers. (Bateson, and Hurst.)

Dendrobium.

Purple, and white (albino) flowers. (Hurst.)

Dianthus.

Single, semi-double, and double flowers in the Carnation. (Norton.)

Digitalis.

Normal, heptandrous, and campanulate flowers in the Foxglove.

Magenta, and white flowers.

Red, and yellow spots of flowers. (Keeble, Pellew, Jones, E. R. Saunders, and Hurst.)

Epilobium.

Red, and white flowers.

Grey-green, and yellow pollen. (Correns.)

Fragaria.

Various characters in *F. virginiana* and *F. elatior*.

Red, and tinged-white fruits of strawberries.

Garden, and alpine forms. (Strasburger, and Hurst.)

Gerbera.

Red, and yellow flowers. (Bateson, and Lynch.)

Geum.

Red, and yellow flowers. (de Vries.)

Gossypium.

Branched, unbranched, tall, and short habit of growth in the Cotton plant.

Early, late, and continuous flowering-habit.

Light green, dark green, red spotted, and faintly spotted leaves.

Glabrous, and hirsute petiole of leaf.

Pointed, and rounded leaves.

Red, yellow, lemon, creamy-white, purple spotted, and unspotted petals.

Tubular, and campanulate corolla.

Long, short, rich-yellow, pale-yellow, and buff-coloured anthers.

Long and short style.

Green, brown, cream, white, long, short, regular, irregular, even, uneven, fine, and coarse lint.

Large, small, fuzzy, naked, loose, and adhering seeds. (Fletcher, Balls, Fyson, and Leake.)

Helianthus.

Branched, and unbranched habit of growth in the Sunflower.

Purple, and yellow disc of flower. (Shull.)

Hordeum.

Lax, dense, hooded, normal, beardless, bearded, 2-rowed, 6-rowed, simple, and compound ears in Barley.

Various degrees of sterility in lateral florets.

Broad, and narrow glumes.

Black, and white paleæ. (Biffen, Tschermak, Johannsen, and John Wilson.)

Hyoscyamus.

Annual, and biennial habit of growth.

Dark, and pale flowers. (Correns, and de Vries.)

Lathyrus.

Tall, bush, prostrate cupid, and erect cupid habit of growth in the Sweet Pea.

Flat, hooded, waved, and snapdragon standards of flowers.

Purple, red, white, cream, crimson, rose-pink, scarlet, orange, salmon, and blue flowers.

Self-coloured, bicolor, picotee edged, and flaked flowers.

Long, and round pollen-grains.

Fertile, and sterile anthers.

Dark, and light coloured seeds and axils of stems. (Bateson, E. R. Saunders, Punnett, Biffen, Cuthbertson, Thoday, and Hurst.)

Linaria.

Orange, and yellow palate of flowers. (de Vries.)

Lunaria.

Green, and variegated (albo-marginata) leaves. (Correns, and Baur.)

Lychnis.

Annual, and perennial habit of growth.

Hairy, and smooth leaves.

Reddish-purple, bluish-purple, and white flowers.

Curved and straight capsules. (de Vries, Bateson, E. R. Saunders, Punnett, and Shull.)

Lycopersicum.

Tall and dwarf habit of growth in the Tomato.

Normal-cut-leaf, entire, tripinnate, smooth, rough, green, and yellow leaves.

Many-celled, 2-celled, round, pyriform, conic, compressed, smooth, tomentose, red, pink, and yellow fruits.

Red, and yellow flesh of fruits.

Yellow, and white skin of fruit. (Price, Drinkard, East, and Hurst.)

Matthiola.

Branched, and unbranched habit of growth in Stocks.

Hoary, glabrous, glandular, and glandless leaves.

Annual, and biennial habit of growth.

Single, and double flowers.

Purple, red, blue, white, cream, sulphur-white, crimson, terra-cotta, flesh, rose, lilac, violet, copper, and plum coloured flowers.

Green, and brown seeds. (E. R. Saunders, Bateson, Punnett, Correns, Tschermak, and Wheldale.)

Melandrium.

Green, and white leaves. (Baur.)

Mimulus.

Normal, and monstrous flowers. (Correns.)

Mirabilis.

Tall, and short habit of growth.

Green, variegated, and yellow (*chlorina*) leaves.

Crimson, yellow, white, pale yellow, magenta, orange-red, white-flaked-magenta, magenta rose, white-flaked-yellow, pale yellow-flaked-yellow, and magenta-rose-flaked-orange-red flower colours. (Correns; Marryat, and Baur.)

Nicotiana.

Purple, red, pink, yellow, and white flowers.

Blue, and grey-white pollen.

Inflated, and funnel-shaped corolla. (Lock, Haig-Thomas, and Hurst.)

Odontoglossum.

Yellow, cream, white, blotched, and plain flowers. (Hurst.)

Œnothera.

Long, and short style.

Rubricalyx, and *rubrinervis* forms. (de Vries, and Gates.)

Papaver.

Tall, and dwarf habit of growth in Poppies.

Purple, red, white, single, and double flowers.

Various colour types and patterns of the "Shirley" Poppy.

Black, and white basal spot in petals of flower. (de Vries, Bateson, Shull, and Hurst.)

Paphiopedilum (*Cypripedium*).

Purple, and albino forms.

Spotted, and striped colour-patterns in the dorsal sepal of the flower.

Yellow, and green plastid colours in the flowers. (Hurst.)

Pelargonium.

Green, yellow-green, variegated (*albo-marginata*), and yellow leaves.

Light red, rose-pink, salmon-pink, tinged white, and pure white flowers. (Baur, and Hurst.)

Petunia.

Single, and double flowers. (de Vries, and E. R. Saunders.)

Phaseolus.

Tall, and dwarf habit of growth in Beans.

Green, and white leaves.

Purple, red bicolor, and white flowers.

Constricted, inflated, stringy, stringless, blunt, pointed, axial, terminal,
green, and yellow pods.

Purple, yellow, brown, orange, dark-red, black, and white seeds.

Size, shape, and weight of seeds.

Self-coloured, bicolor, and mottled seeds.

Hypo-geal, and epi-geal cotyledons. (Emerson, Tschermak, Shull, and
Johannsen.)

Phyteuma.

Violet, blue, and white flowers. (Correns.)

Pisum.

Tall, half dwarf, and dwarf habit of growth in Peas.

Long, and short internodes, thick, and thin stems.

Early, and late flowering and ripening.

Purple, red, and green axils.

Purple, pink, and white flowers.

Distributed, and bunched flowers.

Normal, and fasciated stems.

Green, and yellow unripe pods.

Inflated, constricted, blunt, pointed, wide, and narrow pods.

Round, indent, and wrinkled seeds.

High, and low absorptive capacity of seeds.

Long, round, simple, and compound starch grains in seeds.

Yellow, and green cotyledons.

Dark, and pale hylum of seed.

Purple spotted, reddish dotted, mapled, grey, and white seed coats.

(Correns, Tschermak, Bateson, E. R. Saunders, Punnett, Lock,

Gregory, Darbishire, Keeble, Pellew, and Hurst.)

Polemonium.

Blue, white, and yellow flowers. (de Vries, and Correns.)

Primula.

Palm-leaved, fern-leaved, ivy-leaved, and parsley-leaved forms in the Chinese Primrose.

Dark red, pale red, and green stems.

Pure white, tinged white, flaked white, flesh coloured, salmon-pink, rose-pink, red, crimson, magenta, lavender, and blue flowers.

Small-eyed, large-eyed, dark-eyed, and light-eyed flowers.

Imbricate (*sinensis*), and stellate (*stellata*) petals.

Normal, and giant forms of *stellata*.

Short style with large pollen-grains and "thrum-eye," long style with small pollen-grains and "pin-eye," and homostyled.

Red, and green stigmas.

Petalody of sepals.

Single, and double flowers. (Bateson, Gregory, Keeble, Pellew, and Hurst.)

Prunus.

Hairy, and smooth fruits in Peaches and Nectarines.

Large, and normal flowers.

Reniform glands, round glands, and glandless petioles of leaves. (Rivers, and Bateson.)

Ranunculus.

Spiny, tuberculated, and smooth fruits. (Bateson, E. R. Saunders, and Punnett.)

Salvia.

Purple, red, and white flowers. (Bateson, and E. R. Saunders.)

Secale.

Winter, and Summer varieties of Rye.

Blue-green, and yellow-green grain. (Tschermak, and Ruëmker.)

Silene.

Red, rose, and white flowers. (de Vries.)

Solanum.

Strong, medium, and weak-coloured stems in the Potato.

Normal, and twisted leaves.

Round, oval, and long tubers.

Deep, and shallow-eyed tubers.

Purple, red, and tinged-white tubers.

Coloured, and pure white flowers.

Self-coloured, and tongued-pattern of flowers.

Sterile, and fertile anthers.

Immunity, and susceptibility to disease. (Salaman, and East.)

Trifolium.

Red, and white flowers.

Five-leaved, and three-leaved clover. (de Vries.)

Triticum.

Winter, and Spring habit in wheat.

Thick-hollow, thin-solid, angular, circular, bristly, and smooth stems.

Rough, smooth, broad, and narrow leaves.

Beardless, bearded, compact, and dense ears.

Felted, smooth, keeled, rounded, large, and small glumes.

Red, white, and grey chaff.

Red, white, long-narrow, and short-round grains.

Hard-translucent, soft-opaque endosperms.

Strong, and weak quality of flour.

High, and low yield of grain.

Early, and late ripening of grain.

Susceptibility and immunity to yellow rust. (Spillman, Tschermak,

Biffen, John Wilson, and Nilsson-Ehle.)

Tropæolum.

Tall, and dwarf habit of growth.

Red, and yellow flowers. (Weiss.)

Ulmus.

Opposite, alternate, small, and large leaves.

Long, and short petioles in the Elm. (Henry.)

Urtica.

Much serrated, and little serrated edges of leaves in the Nettle.

Green, and yellow-green (Chlorina) leaves. (Correns, and Baur.)

Verbascum.

Yellow, and white flowers. (Shull.)

Veronica.

Blue, and white flowers. (de Vries.)

Viola.

Dissected, undissected, pubescent, and glabrous leaves in the Violet.
Blue, and white flowers.
Purple, and green capsules.
Brown, buff, black, and pale yellow seeds. (de Vries, and Brainerd.)

Zea.

Flint, dent, and sweet corn in Maize.
Purple, white, yellow, and red seeds.
Large, and small grains.
Long, and short stalks. (de Vries, Correns, Lock, East, Shull, and Emerson.)

(b) ANIMALS.

Abraxas.

Typical, light (*lacticolor*), and dark (*Varleyata*) forms of moth in
A. grossulariata. (Currant Moth.)
Female, and male sex. (Doncaster, Raynor, Bateson, and Newman.)

Amphidasys.

Black (*doubledayaria*), and typical forms of moths in *A. betularia*
(Peppered moth.) (Bateson, Main, and Harrison.)

Aglia.

Dark (*lugens*), and typical forms of moths in *A. tau*. (Bateson, Standfuss, and Castle.)

Angerona.

Dark-banded (*sordiatu*), and typical-reticulated forms of moths in
A. prunaria. (Doncaster.)

Arion.

Black, brown, red, and striped slugs. (Collinge, and Cockerell.)

Athene.

Yellow, and black eyes in *A. noctua* (Little Owl). (Bateson, and Giglioli.)

Axolotl.

Dark, and light larvæ. (Häcker.)

Bombyx.

Dark, and light moths in *B. mori* (Silkworm).

Dark, white, self-coloured, light-striped, and dark-striped larvæ.

Black, red, blue, and brindled worms.

Salmon-coloured cocoons.

Yellow, and white silk. (Contagne, Toyana, and Kellogg.)

Bos.

Polled, and horned cattle.

Red, black, red-roan, blue-roan, white, brown, brindled, dun, and yellow coat-colours in Cattle.

White face in Hereford cattle.

White back-stripe in Longhorn cattle.

Long, and short faces.

Stout-short-legged, and slender-long-legged breeds. (Dexters and Kerries.)

Hollow, and round rump. (Shorthorn and Angus.) (Bateson, Spillman, and James Wilson.)

Callimorpha.

Red, and yellow hind wings in *C. dominula*. (Bateson, Standfuss, and Newman.)

Canis.

Black, and red coat-colour in Retriever dogs.

Brindle, and wheaten coat in Scottish terriers. (Hurst.)

Capra.

Horned, and hornless goats. Lop (Indian), and Erect (Irish) ears.

Presence, and absence of neck-wattles. (Bateson, Boys-Smith, and Davenport.)

Cavia.

Short, and long (Angora) hair in Guinea-pigs.

Rough-rosetted (Abyssinian), and smooth coats.

Agouti, yellow-agouti, silver-agouti, black, blue, red, black-red, yellow, cream, cinnamon, yellow-cinnamon, silver-cinnamon, chocolate, and silver-fawn coat-colours.

White with black points, white with chocolate points, white with red points (albinos).

Brindled, and spotted coat-colour patterns.

Dark, ruby, and pink eyes. (Castle, Forbes, Sollas, and MacCurdy.)

Coccinella.

Red, and melanic types. (Johnson.)

Columba.

Normal, and webbed feet in pigeons.

Plain head, and "shell" feathers. (Nun.) Blond, and white doves.

Barb and Tumbler black, blue (Rock), red, Tumbler-white, Fantail-white, black and white, blue and white, ticked white, and tricolor plumage.

Chequered, blue, and white rumps.

Pigmented, and unpigmented beaks and claws.

Red, and flesh-coloured eye-wattles.

White ("pearl"), orange, and black ("bull") eyes. (Staples-Browne, Hurst, Bond, Bonhote, Strong, and Cole.)

Crioceris.

Dark, and light forms of Asparagus Beetles. (Lutz.)

Drosophila.

Long, short, veined and scalloped wings of Vinegar Flies.

High, and low productiveness, dwarfness.

Red, and white eyes.

Male and female sex. (Morgan, Lutz, Castle, Carpenter, Clark, Mast, and Barrows.)

Equus.

Trotting, and pacing gait in horses.

Bay-brown, shire-black, liver-chestnut, yellow-chestnut, white-grey, roan-grey, and dun coat-colours.

Concave, and convex faces.

Straight, and curved thighs and hocks.

Prick-ear, drooping-ear, forward-droop, and outward-droop of ears.

Sprinters, and stayers.

Liability to cataract-blindness, breaking blood-vessels, and paralytic roaring.

Long-back, and short-back. (Bateson, Robertson, James Wilson, Bunsow, and Hurst.)

Felis.

Short, and long (Persian) hair in Cats.

Short (Manx), and long tail.

Red, cream, black, blue, and tortoise-shell coat-colours.

Striped, and blotched tabby-patterns. (Doncaster, Bateson, Davenport, Pocock, and Hurst.)

Gallus.

Rose, pea, single, walnut, Y, V, Breda, and silky combs.

Leghorn, Dorking, Wyandotte, Rock, Silky, Rosecomb-Bantam, Andalusian, Breda, and other dominant and recessive kinds of white plumage.

Black, and blue plumage of Andalusians and Bredas.

Buff, black, and red plumage of various breeds.

Self-coloured, barred (Cuckoo), pencilled, spangled, laced, mottled and pile patterns of plumage colour.

Gold and silver-Duckwing patterns.

Black and white Crests.

Brown-striped, and pale brown down-colour.

Crested, muffed, bearded, and plain-heads.

Normal, extra-toed, vulture-hocked, rumpless, wingless, and web-footed birds. Cerebral hernia, low-narrow, and high-wide nostrils.

Plain, silky, and frizzled feathers.

Red, and white ear-lobes.

Red, black, dark brown, pearl, and daw eye-colours.

Black, white, yellow, willow, and horn-coloured feet, shanks, and mandibles.

White, yellow, blue, and silky-black skin-colour.

Shrieking, and non-shrieking voices.

Broody, and non-sitting habits. (Bateson, Punnett, Davenport, Spillman, Pearl, Surface, Goodale, and Hurst.)

Gastroidea.

Blue-black, and bright-green forms of *G. dissimilis*. (McCracken.)

Gryllus.

Wing dimorphism in *Gryllus*. (Lutz.)

Helix.

Unbanded, and five-banded types of snails (*H. hortensis* and *H. nemoralis*).

Yellow, red, and brown ground-colour. (Lang.)

Hemerophila.

Dark-coloured variety, and type in *H. abruptaria*. (Bateson, and Harris.)

Hippodamia.

Spotted patterns of elytra in *H. quinquesignata*, *lecontei*, *convergens*, *extensa*, and *glacialis*. (Johnson.)

Leptinotarsa.

In the Colorado Potato-beetle, typical *L. decemlineata* and its varieties *pallida*, *melanicum*, *tortuosa*, and *rubrivittata*.

Typical *L. multiteniata* and its varieties *melanothorax* and *rubicunda*. (Tower.)

Lepus.

Short fur, and long (Angora) hair in rabbits.

Grey, black, white-tailed-yellow (Silver Fawn), blue-tailed-yellow (Tortoiseshell-Dutch, and Sooty Lop), blue-grey (Dutch), blue (Dutch), cream, blue-fawn (Dutch), and pale-sooty (Lop), coat-colours.

Pure-white (Polish), and Himalayan-white albinos.

English-spotted, Self-coloured, Dutch marked, spotted Dutch, and black and tan coat-colour patterns.

Plain, and silvered-coats.

Fertility and partial sterility in Lops. (Castle, Punnett, and Hurst.)

Lasiocampa.

Red, and white fur (larval hairs) in *L. quercus sicala* and *L. q. meridionalis*. (Bateson, Bacot, and Warburg.)

Lina.

Spotted, and self-coloured-black elytra in *L. lapponica*. (McCracken.)

Melasoma.

Spotted, intermediate, and self-coloured-black elytra in *M. scripta*. (McCracken.)

Mus.

Agouti-grey ("brown"), Alexandrian-black, Norway-black, and albino coat-colours in Rats.

Irish, hooded, and self-coloured coat-colour patterns in Rats.

Hairy and naked skin in Mice.

Normal and waltzing Mice.

Yellow, grey (agouti), black, chocolate, cream, blue-grey, pale-grey (Chinchilla), blue, pale-blue, cinnamon, pale-cinnamon, pale-chocolate, lilac, pale-lilac, and pure white (albino) coat-colours in Mice. Self-coloured, dominant piebald, and recessive piebald coat-colour patterns in Mice.

Black (dark-brown), ruby (chocolate), and pink eyes in Mice. (Bateson, Doncaster, Mudge, Morgan, MacCurdy, Castle, Campbell, Darbshire, Allen, Cûénot, Durham, Little, Schuster, and Hagedoorn.)

Numida.

Pearl-coloured, and white plumage in Guinea-fowls. (Davenport.)

Ovis.

Horned, and hornless sheep.

White, and black wool.

White, black, and speckled faces.

Woolly, and bare heads.

Black, blue, and white, skin and faces in Wensleydale sheep.

Normal, and otter breed (Ancon). (Wood, Bateson, Davenport, Robertson, and Dwight.)

Serinus.

Full crested, half crested, plain-headed, and bald-headed canaries.

Green, cinnamon, "Jonque," and "Mealy" plumage-colour.

Clear, pied, mottled, and ticked colour-patterns.

Lizard-cap-and-lacings, shoulder-striping, black-wing, olive-breast, and white-laced remiges.

Black, and pink (juvenile) eyes.

Male, and female sex. (Bateson, Davenport, Noorduijn, and Durham.)

Sus.

Yorkshire-white, Berkshire-black, and Tamworth-red colours in pigs.

Self-coloured-black, and white-belted-black (American) colour-patterns.

Mule-foot, and normal feet. (Spillman, Bateson, Staples-Browne, and Simpson.)

Triphæna.

Melanic, and reddish forms of *T. comes*. (Bateson, Bacot, and Prout.)

Xanthorhœ.

Purplish-banded, and black-banded forms of *X. ferrugata*. (Doncaster and Prout.)

(c) MAN.

Brown (Self Duplex), grey (Ringed Duplex), and blue (Simplex), eye-colours.

Fiery-red, auburn (brown-red), and flaxen (yellow) hair colours.

Straight, wavy, and curly hair-forms.

Dark (Brunet), fair (Blond), and intermediate skin-colours in "white" races.

Various grades of skin-colours in mulattoes and "whites."

Pale, fresh, and coloured complexions in "white" races.

Normals, and various grades of "albinos" in black and "white" races.

Short, and tall stature in Filipinos.

Round, and long heads in Filipinos.

Broad, and narrow noses in Filipinos.

Non-musical, and musical temperaments.

Immunity, and susceptibility to various kinds of diseases.

Various inherited deformities and defects.

Dominant hereditary malformations and diseases include: Brachydactyly, aborted fingers, split-hand and split-foot, Cataract, Tylosis palmaris et plantaris (Keratosis), Epidermolysis bullosa, Xanthoma, Multiple Telangiectasis, Hypotrichosis congenita familiaris, Monilithrix, Porokeratosis, Enlarged spleen, Diabetes insipidus (polyuria), Hermaphroditism, Hereditary Chorea, Stationary night-blindness, and the Sex-linked diseases, Hæmophilia, Colour-blindness, Pseudo-hypertrophic muscular paralysis (Gower's Disease), and certain kinds of night-blindness.

Recessive hereditary diseases include Retinitis pigmentosa, alkaptonuria, certain forms of Deaf-mutism, Insanity, and Imbecility.

(Farabee, Bateson, Punnett, Davenport, Gossage, Drinkwater, Mudge, Nettleship, Garrod, Bean, Grover, and Hurst.)

The above list will serve, better than any words of mine, to illustrate the great and growing importance of Mendel's discovery, and will give the general reader some idea of the remarkable developments that have taken place during the last few years in the application of Mendelism to plants, animals, and man. Thanks largely to the labours of Bateson and his co-workers, a new science—the science of Genetics—has been built up on a Mendelian basis. This science, with its modern methods of factorial analysis, and pure-line breeding, promises to provide solutions to many problems of heredity and variation hitherto obscure.

Notwithstanding the short time that has elapsed since Mendel's memoir was discovered, the influence of Mendelism is already being felt, not only in the academic world of Biology, but also in the practical Arts and Industries related thereto.

In the ancient arts of Agriculture and Horticulture, for instance, new races and strains innumerable are being built up and isolated by the aid of the Mendelian principles, and it is impossible to estimate the vast economic results that may arise therefrom.

In the old science of Medicine and the new science of Eugenics, the Mendelian principles have already, in certain cases, shed a clear light where before was utter darkness.

In the systematic sciences Botany, Entomology, Ornithology, and Zoology, systematists are already beginning to utilise the Mendelian principles to assist them in the determination of their species and varieties.

The influence of Mendelism in modifying the Darwinian conceptions of Evolution, is already considerable, and the reflex of this influence must, sooner or later, be felt in the more remote regions of Philosophy.

XXVI

THE GOVERNMENT GRANT FOR HORSE-BREEDING¹

THE QUESTION OF EUGENICS

In reviewing the present condition of national horse-breeding it is evident that, so far as pure breeds are concerned, this country has reason to be proud of its position. Our pure breeds of horses are acknowledged to be the best in the world, and our pedigree animals are the desire of all nations. This applies both to light and heavy horses, whether they be Thoroughbreds or Shires, Hackneys or Clydesdales, Yorkshire coach-horses or Suffolk Punches.

But when we come to consider the most useful type of saddle horse, the hunter, the state of things is very different. The cause of this is not far to seek, for hunter breeding, as carried out on the present lines, is acknowledged by all men of experience to be of the nature of a lottery, with a few prizes and many blanks—or rather a multitude of unprofitable “misfits.” Consequently, farmers and breeders have largely given up the industry, and have taken up the more profitable cart-horse. This economic result, though deplorable from many points of view, would not necessarily be a serious national loss, were it not for the fact that the War Office has very largely relied on the purchase of these hunter misfits for Army purposes. Owing to the reduced supply the military authorities have lately experienced some difficulty in securing enough saddle-horses suitable for their purpose. Further, the experience of the South African War showed the vital necessity of retaining in this country a large reserve of horses suitable for military purposes, over and above the 3000 or so required annually for the peace establishment. It is evident, therefore, that, apart altogether from economic considerations, the decay of hunter breeding in this country has become a matter of urgent national importance.

¹ Communicated to *The Times*, March 4th, 1911, at the request of the Editor.

Fortunately, at such a critical moment, Lord Carrington and his advisers at the Board of Agriculture have seized the opportunity presented by the Development Grant, and succeeded in obtaining from the Treasury a grant of £40,000 a year for the encouragement of light horse-breeding in this country. A scheme has been drawn up by the Board, and Lord Carrington has appointed an advisory council of experts, under the chairmanship of Lord Middleton, to assist the Board in making the scheme a success. It is understood that the advisory council will in future take over the duties of the Royal Commission on Horse-Breeding; and it is satisfactory to know that, in order to ensure continuity, five members of that Commission have been appointed to the advisory council. As a further sign of the times, it is interesting to note that, in addition to two veterinary experts, the services of two experts in experimental heredity have been secured to watch the operations of the Board from the point of view of scientific research in eugenics as applied to horses. So far everything possible seems to have been done to command success.

We may now proceed to consider the scheme for 1911 as proposed by the Board:—

(1) *King's Premiums.* 50 King's Premiums are being offered to the best class of thoroughbred stallions at the Hunter Show at Islington; these stallions will serve in 19 districts in Great Britain. It is understood that 115 stallions have already been entered to compete for these premiums.

It is peculiarly gratifying to know that his Majesty the King has shown such interest in the scheme that he has been graciously pleased to offer a Challenge Cup to be competed for by the winners of the King's Premiums.

(2) *Board Premiums.* 50 Board's Premiums are also offered for stallions, not necessarily thoroughbred; these stallions will be selected by the Board, with the assistance of the local committees, which are to be formed in each county.

(3) *Free Nominations.* In order to encourage the keeping of brood-mares in this country, the Board propose to give about 1400 free nominations to suitable mares through the agency of the county committees, preference being given, so far as possible, to small occupiers possessing a good class of mare, who otherwise might be expected to use an inferior stallion.

(4) *Purchase of Brood-mares.* The Board also propose to purchase some 200 half-bred active working mares, to be placed with suitable

persons by the county committees. These mares will be served by a premium stallion, and county committees will have the option of purchasing any of the foals up to four years old.

(5) *Purchase of Stallions.* On the recommendations of the Royal Commission and the Hunters' Improvement Society, the Board propose to take the power to purchase any valuable stallions which would otherwise be exported and lost to the country. It is understood, however, that no money will be used for that purpose this year.

(6) *Registration of Stallions.* The Board also propose to invite owners to register any pure-bred stallion—light or heavy—which is entered in the Stud Book of its particular breed, subject to its being passed sound for breeding purposes.

Of the general effect of the Board's scheme in encouraging the breeding of light horses there can be no manner of doubt. The distribution of 100 sound stallions of quality throughout the country is bound to improve and increase the horse supply. The distribution of 1400 free nominations will give the farmer an inducement to use the premium stallion in preference to an inferior one. The distribution of 200 brood-mares will induce farmers to breed who otherwise would probably not do so. The registration of stallions of all breeds should tend to make the use of an unsound stallion unprofitable, and thus increase the number of sound horses in the country.

On the whole, therefore, the Board's scheme for 1911 has much to commend it; and, if wisely administered, it should go far to revive a dying industry and at the same time replenish our reserve of horses for a national emergency.

To be permanently successful, however, it is obvious that such a scheme must be kept going each year; and the question naturally arises whether it may be regarded as in any sense a final or permanent remedy for the specific evil, or whether it should be regarded merely as a palliative for the time being. It seems worth while to consider whether it might not be advisable to spend a portion of the grant on such a scheme, and invest the remainder in some definite scientific experiments, which in course of time should go far to remedy the evil and ultimately make the whole grant unnecessary.

Amid all the multitudinous ideas and conflicting opinions about light-horse breeding, there is one point upon which all seem to be agreed, and that is that the type of saddle-horse wanted in this country is the weight-carrying hunter. All, too, agree that this type of horse cannot be bred with any degree of certainty on the present lines. The

solution of the whole problem would appear therefore to lie in the possibility of establishing a true breed of hunters that could be relied upon to breed true to type and character, like the Shires, Clydesdales, and Suffolk Punches. If this object could be attained, hunter-breeding would soon become a profitable industry which the farmer would be only too pleased to take up, our Army would be better mounted, and a sufficient reserve of horses suitable for military purposes would be maintained in the country ready for any emergency. The Hunters' Improvement Society has in recent years taken up this question with great courage and credit to all concerned. A Hunter Stud-Book has been formed, and various sires and brood-mares have been registered therein as hunters. Unfortunately their well-meaning enthusiasm has caused them to reverse the natural order of things. Instead of fixing the breed in order to make a stud-book they seem to have made a stud-book in order to fix the breed. Consequently their efforts have been rewarded by but partial success, and the true breeding hunter remains still to be found.

It is to be hoped, therefore, that the Board of Agriculture and its advisory council will take the opportunity presented by the Government grant to institute some definite scientific experiments in order to solve the problem of the formation of a pure-breeding hunter. Ten years ago such a problem might well have been regarded as insoluble; but, since the discoveries of Mendel have been made known and the remarkable advances that have been made in our knowledge of breeding by recent experiments with many kinds of animals and plants, such a problem as the creation of a pure-breeding hunter seems to be quite within the bounds of practical politics. If the Board decide to carry out some scientific experiments, the question of the establishment of an experimental breeding station or a Government stud-farm might have to be considered. In any case, the experiments would have to be carried out under the personal supervision of the scientific experts appointed by the Board, who would draw up the scheme and carefully record the results. Fortunately Mendelian experiments deal with small numbers of individuals rather than with large masses, so that there would be no need to conduct the experiments on a large and expensive scale.

In the production of a breed of hunters some sort of a test would no doubt be required both for the foundation parents and also for their offspring. With regard to this it is to be hoped that too much weight would not be attached to the winning of prizes at hunter shows.

However desirable it may be to have a breed of handsome hunters, it is still more important that they should be bred so as to be able to hold their own in a fast run across a big country or win a long-distance steeplechase under a welter weight. Soundness, action, good temper, and build may, of course, be equally well tested in the show-ring; but speed, staying power, weight carrying, and cleverness would be better tested between the flags or in the hunting field. Another important point apt to be overlooked by breeders has been greatly accentuated by the results of recent Mendelian experiments—and that is, that the outward appearance, or even the good performance, of an animal is not necessarily any guide to its breeding potentialities.

The only safe test of a stud animal is the stock which it produces; however good-looking it may be or whatever good it may have done, it is no good for high-class breeding purposes unless it is known to have thrown good stock. This, after all, is only simple common sense, and yet it is curious to observe how few breeders there are who strictly act upon it. If such tests as these were to be applied at the Hunter Show at Islington, one imagines that many of the show winners would fail to get a card and few stallions would gain their premiums.

All this goes to show the vital necessity of applying Mendelian methods to the breeding of stock. No rapid progress may be expected until the new knowledge is fully grasped by the breeder. As a demonstration of what it is and what it means, nothing could be better than a few simple experiments with a practical issue, carried out by the Board of Agriculture and its advisory council with the aid of a small portion of the Government grant. The introduction of eugenics to horse-breeding would not be the least of the many services rendered to agriculture by the Board under its present chief.

XXVII

THE APPLICATION OF GENETICS TO HORSE-BREEDING¹

Soon after the discovery of Mendel's work in 1900, my attention was directed to the thoroughbred horse as a promising subject for investigation. The question of coat-colour provided a useful beginning. A few years' investigation of Wetherby's *General Stud-Book* brought to light the fact that chestnut coat-colour is recessive to bay and brown. Consequently chestnut horses always breed true when mated together, notwithstanding their possible bay and brown parents and ancestors. On the other hand, bay and brown horses are of two kinds, either they throw chestnuts or they do not².

Further investigation showed that grey coat-colour is dominant to bay, brown, and chestnut. Consequently every grey horse must have a grey parent and a grey ancestor in every generation in the direct line. In England grey thoroughbreds are few, and grey \times grey matings are rare, consequently English grey thoroughbreds are nearly all heterozygous, throwing bays, browns, or chestnuts. Mr R. Bunsow has found a homozygous grey in Germany, the Arabian stallion, Celle Amurath, which throws nothing but greys³.

The genetic relationships between bay and brown, and between grey and roan, are not yet known.

With regard to black, Professor James Wilson has pointed out that in thoroughbreds all the so-called "blacks" are really dark browns with tan muzzles.

In the Shire and the Clydesdale, however, Professor Wilson finds true blacks, which apparently behave as dominants to chestnuts, and probably as recessives to bays, browns, and greys⁴.

With regard to chestnuts, it seems likely that several genetic types

¹ Read before Sub-section "K" (Agriculture) at the Portsmouth Meeting of the British Association for the Advancement of Science, August 1911, and reprinted from the Annual Report (1911).

² See *Proc. Roy. Soc.* 1906, B, LXXVII. p. 388. (See p. 239.)

³ *Mendel Journal*, No. 2, 1911, p. 89.

⁴ *Proc. Roy. Dubl. Soc.* XII. (N.S.), No. 28, 1910, p. 337.

may exist. Mr J. B. Robertson has pointed out that the dark or liver chestnut behaves as a dominant to the light or yellow chestnut.

To the practical breeder the question of coat-colour is a minor consideration, except, perhaps, in a few fancy breeds where certain colours are more popular than others. In the thoroughbred, at all events, a good horse is of any colour. A much more important question is: Can he win the Derby?

Coat-colour and Racing-power.

Generally speaking, coat-colour and racing-power do not seem to bear any sort of relationship to one another, being apparently inherited quite independently. On the other hand, evidence is gradually accumulating which suggests that, *in certain strains*, there is a partial coupling of coat-colour and racing-power.

For instance, the famous St Simon was a homozygous bay that never threw a chestnut. On the other hand, five of his most distinguished sons—Persimmon, Diamond Jubilee, Florizel II, St Frusquin, and William III—were all heterozygous bays and browns that threw chestnuts. These chestnut grandchildren of St Simon have so far proved themselves to be much inferior in racing-power to their bay and brown brothers and sisters. Thus, while these chestnuts have between them only won two classic races, their bay and brown brothers and sisters have between them won fifteen classic races, and are only about twice as numerous.

Another interesting point under investigation is the apparent partial *tripling* of brown coat-colour, high racing-power, and female sex in St Simon's own offspring. St Simon's brown fillies proved themselves to be strikingly superior in racing-power to the bay fillies, the brown colts, and even to the bay colts, a few individuals of which were extraordinarily good. This is the more remarkable when we consider that in racing colts have many advantages over fillies.

It seems possible that the elucidation of such an apparently trivial thing as coat-colour may help to throw light on the more complicated question of the breeding of a classic winner.

Homozygous Hunters.

It is generally admitted that the most useful type of light horse is the hunter. Recently Professor Cossar Ewart and I have drawn up a scheme of experiments in horse-breeding for the use of the Board of Agriculture, the object being to make a line of homozygous hunters.

At present there is no such thing as a pure-breeding hunter; our studies have been mainly based on the thoroughbred 'chaser as probably the most suitable material upon which to work.

Our investigation of the Stud-Book and Racing Calendar to find suitable animals with which to experiment has led us to the discovery of the existence of homozygous 'chasers, though in very few numbers. After eliminating many hundreds of heterozygous and doubtful animals, we have found five mares and three stallions, which, when bred together, have given nothing but horses of the 'chaser type, as tested on the race-course and at the stud.

In view of this fortunate find of what might perhaps be called a 'chaser "pure line," we have recommended the Board of Agriculture to purchase some of the offspring of these animals, in order to increase the "pure line," and we hope that this experiment will help us to solve the problem of the making of a homozygous hunter.

XXVIII

THE APPLICATION OF THE PRINCIPLES OF GENETICS TO SOME PRACTICAL PROBLEMS¹

The new Science of Genetics, so faithfully christened by Bateson at our last conference, has been founded on the wonderful work of Mendel. The development of the new Science has recently been so rapid, that in many respects it has quite outgrown its Mendelian infancy and simplicity. It is indeed fast taking on the more complex strength and beauty of vigorous youth, equally unspoiled by tradition and untrammelled by convention. The time is now at hand therefore, when the important question of its usefulness in life, may be fairly asked of it. An older Science might resent such a question and scornfully reply, "Truth for Truth's sake." But not so our new world science, filled with the Spirit of the Age which requires even Truth to be efficient. The efficient application of pure Science to the practical problems of life, is in any case a matter of considerable difficulty, and this is particularly so with such a Science as Genetics. In the first place comes the necessary appreciation of the significance of the practical problem to be solved. This can only be attained by years of intimate practical experience, usually impossible to the Man of Science. In the second place comes the equally important first-hand knowledge of research in the pure science concerned. This can only be secured by years of scientific study and experience, usually impossible to the practical man. It is evident that the opportunities of efficiently applying pure Science to the practical problems of life, are few and far between. A great responsibility therefore rests on those individuals who happen to be placed in circumstances where scientific research and economic work can be happily combined.

With this object in view, the Burbage Experiment Station has been established, for the application of the principles of Genetics to some

¹ Read at the Fourth International Conference on Genetics, Paris, September 1911, and reprinted from *Rep. Conf. Nat. Hort. Soc. de France* (1913).

practical problems of Agriculture, Horticulture, and Forestry, on an extended scale, and in the following report a slight sketch is given of the practical problems that have been undertaken at the station.

Culinary Peas. In Culinary Peas, perhaps the most pressing practical problem to be solved, is the frequent appearance of "rogues" amongst some of the best and most carefully selected varieties. Some of these are undoubtedly due to accidental mixture during process of harvesting, cleaning, and so forth. A few might possibly be due to cross fertilisation by insects, though in view of the peculiar structure of the flowers such cases must be exceedingly rare. Out of 112 varieties tested at the Station this summer, no less than 33 threw "rogues" notwithstanding that all the stocks were obtained from the most reliable sources. One particular kind of "rogue" appeared persistently in many different dwarf wrinkled varieties. It was easily distinguished by its thin, vetch-like haulm, 1½ ft. high, short internodes, small leaves and flowers, small curved pods containing medium-sized green wrinkled seeds. Steps have been taken to investigate the nature of this "rogue," the cause of its appearance, and the possibilities of its elimination.

In the cultivation of culinary peas great importance is naturally attached to the question of earliness, and it may be interesting to note that this summer in the 112 varieties (all sown within 3 days) there was a range of difference of 52 days, in the time of ripening for culinary purposes.

The question of yield is a most important economic consideration.

The heaviest croppers appear to be those varieties which bear the largest number of pairs of pods. Recent results show that this is more apparent than real.

Some varieties *e.g.* "Velocity" seem to bear no pairs at all, while others bear different proportions of pairs to singles. Thus for instance, among those counted on individual plants,

20 plants of Velocity	gave	0 pairs and	202 singles,
20 " Peter Pan	" 4	"	471 "
27 " First of All	" 7	"	358 "
35 " Primo	" 11	"	459 "
31 " William 1 st	" 66	"	749 "
40 " Eight weeks	" 93	"	648 "
20 " English Wonder	" 142	"	593 "

These facts suggest that the tendency to produce more pods in pairs is inherited, and there seems to be no reason why the application of

the methods of genetics to this problem should not prove effective. Altogether, this year, 521 plants of selected varieties of culinary peas have been grown singly, and their seeds saved separately with the object of raising homozygous lines from which all rogues have been permanently eliminated, and which will bear a larger proportion of their pods in pairs.

The solitary appearance in the $6\frac{1}{2}$ acres of trials, of a single green pod containing 5 peas with purple-tinged seed-coats is recorded.

Whether these seeds are pathological or normal remains to be seen.

At present they seem to be sound, though rather smaller and more wrinkled than their fellow seeds on the same plant. Their future behaviour will be looked forward to with some interest.

Sweet Peas. Sweet Peas differ from Culinary Peas in the fact that their development during the last few years has been extremely rapid, indeed it is somewhat difficult to keep pace with the various practical problems that have arisen so quickly and unexpectedly. The introduction of the popular waved flowers known as the "Spencer" Sweet Peas, has created a revolution in Sweet Pea growing, and many of the "grandiflora" hooded varieties, so popular a few years ago, are now entirely superseded, while the old-fashioned forms with plain erect standards are quite obsolete.

It is interesting to note how quickly practical breeders have taken advantage of Mendelian research and have thus been able to raise waved forms of the old "grandiflora" types in a very short time (fig. 119). One difficulty however seems to have been encountered, and that is that certain dark blue shades of colour, of the "Lord Nelson" type do not seem to take on the true waved form as other colours do.

The question of the desirability of raising varieties with double standards is still a moot one with Sweet Pea fanciers. It would appear however that some difficulty may be experienced in raising such forms true to type, for I notice that most of the flowers with double standards have an exposed pistil, these are more likely to be cross-fertilised by insects, and in any case may require to be fertilised by hand to set many seeds. Further observation shows that the more wavy the flower, the more the pistil is exposed, and this may possibly account for the extraordinary number of rogues that now occur in the most carefully selected strains of the best modern varieties. This summer I had the pleasure of visiting the National Sweet Pea Society's trials at Sutton Green, and out of a total of 260 stocks sent by the leading growers, no

less than 99 contained "rogues." In our Mendelian Experiments with the old erect and hooded forms, we found only a few "rogues" caused probably by the bee *Megachile*.

It would appear however that in the modern waved forms the "rogues" are far more numerous, and it is possible that in the future the question will have to be faced, as to the necessity of covering the flowers to secure true stocks, and further of hand-fertilising the flowers to secure a good crop (cf. pp. 421-433).

An interesting form of Sweet Pea has been observed at the Station this summer, in which the standards of the flowers are divided into three distinct lobes, an apical lobe with two basal side-lobes, not unlike a Shamrock leaf. Steps are being taken to breed from this form which has appeared in all the flowers of one plant. Out of 117 varieties of Sweet Peas tested at the station this year, 20 have been selected for further work, and 363 individual plants have been grown separately and their seed saved individually in order to secure, if possible, homozygous lines.

Orchids. The important and complicated question of raising hybrid albinos true from seed, has been much simplified by the application of the Genetic principle that colour may be due to the simultaneous presence of two complementary factors.

In the light of recent results, we are now able to classify many individual albinos, with some confidence, as pure C, pure R, and impure C albinos. In order to obtain hybrid albinos true, all we have to do is to mate the pure C albinos with other pure C albinos, and the pure R albinos with other pure R albinos. On the other hand if the C albinos are mated with the R albinos, coloured forms will undoubtedly result, and our object will not be attained. All this goes to show the importance of adopting some simple method of identification for individual albinos that are used for stud purposes. (For details see pp. 294-299.)

The solution of the present-day problem of raising a scarlet "crispum," or a scarlet Cattleya would no doubt be much hastened by a simple application of the principles of Genetics. To be successful, it will no doubt be necessary to have the scarlet colour and the large size represented in the gametes of both parents. In the case of the scarlet "crispum," such a cross as *Odontioda* × *Vuylstekeæ* (*Odontoglossum nobile* × *Cochlioda Nætzliana*) (fig. 150), mated with *Odontioda* × *Bradshawiæ* (*O. crispum* × *C. Nætzliana*) (fig. 154) should give the desired result in about 1 out of 16 plants raised, provided the case is a simple one. In order to get rid of the purple tinge, it would be well to use

O. nobile album and *O. crispum xanthotes* for the original grandparents, as these albinos are known to breed true when crossed (p. 296).

The fact of the existence of a certain amount of self-sterility in many orchids, makes breeding somewhat more complicated than in other plants. For instance, for several years I have been attempting to self certain segregates of *Cypripedium* \times *Hera*, and so far the only positive result obtained has been 1 plant raised from *C.* \times *Hera punctatum*, and an apparently good pod of seed now developing on *C.* \times *H. Hurstii*. More than 150 selfings have given no good seeds (fig. 91).

Primula. A homozygous line of Giant Star Primulas with pink flowers, cut petals, chocolate eye, fern leaves and red stems, has been obtained in F_5 of a cross between *P. sinensis* and *P. stellata*. The original parents were a white "sinensis" with fern leaves and green stems, crossed with a pink "stellata" with palm leaves and red stems.

F_1 were all light purple, imperfect "sinensis" with palm leaves and red stems. F_2 segregated into a medley of forms, with white, tinged white, pink, light purple, purple, "sinensis," imperfect "sinensis" and "stellata" flowers, palm and fern leaves, and red and green stems. A pink "stellata" with palm leaves and red stems was selfed and gave in F_3 18 pink "stellata" with palm leaves and red stems, 9 the same but with cut petals, 5 pink "stellata" with fern leaves and red stems, 1 the same but with cut petals, and 1 pink stellata with palm leaves, red stems, cut petals, chocolate eye and *giant flowers*. This last plant was selfed and gave in F_4 33 plants of pink "stellata" with cut petals, chocolate eye, *giant flowers* and red stems, of which 22 had palm leaves and 11 fern leaves.

One of the fern leaved plants was selfed and gave in F_5 112 plants of pink "stellata" with cut petals, chocolate eye, *giant flowers*, fern leaves and red stems. These bred true in F_6 .

In this way a new form of Giant Star Primula came into existence and breeds perfectly true in accordance with the principles of Genetics.

Antirrhinum. A number of selected plants of the new shades of colour in Snapdragons of intermediate height, known in gardens as Coccineum, Firefly, Daphne, Nobile, Gloriosum, Niobe, Sunset, Aurora, Black Prince, Dainty Queen, Buff Queen, and Maize Queen, have been selfed with the object of obtaining homozygous lines free from "rogues," which in the best of stocks are far too common. Cuttings of the original plants have also been taken for comparison of parents and offspring next year. The inheritance of the peculiar speckled and striped forms is also being studied (cf. p. 315).

Roses. The best garden roses are more easily raised from buds than from seeds, and no advantage would probably be gained by attempting to raise pure seedling lines. It would appear therefore that the application of genetics should be directed to the raising of new and improved varieties. In order to clear the way for this, and to know precisely what to use as parents so as to attain a definite result, it is necessary first of all to ascertain the gametic composition of the best garden varieties: 350 distinct varieties of all classes have been grown at the Station this year, and 60 of the best of these varieties, representing the Hybrid Perpetual, Hybrid Tea, Tea, Climber and Rambler classes have been selected for seeding. Naturally some years must elapse before any definite results can be recorded.

There is however another problem of great importance to nurserymen, which the science of genetics can help to solve, and that is the raising of certain homozygous lines of Seedling Briar Stocks, on which to work Hybrid Teas and Teas. The present practice is to raise stocks from seeds collected promiscuously from various wild forms of *Rosa canina*, *rubiginosa*, etc. The variability of these forms is well known, and the result is that about 50 per cent. of the stocks raised are unsuitable for the purpose. Consequently the waste is considerable, and the nurseryman only gets about half a crop of Rose trees.

On the other hand a crop of Rose trees worked on the uniform Manetti Stock (raised from cuttings) usually yields a full crop of healthy plants. But only the Hybrid Perpetuals and a few Hybrid Teas will thrive on the Manetti, and the Dog Briar must be used for the best of the Hybrid Teas and Teas.

The problem therefore is to select a vigorous smoothwooded seedling Briar with upright habit and straight stem, and raise a homozygous line of this which will provide a uniform stock suitable for working the choicer varieties of roses upon. We have raised 100,000 seedling Briars at the Station from which we are selecting this year certain special types to breed from, in the hope of obtaining a homozygous line of stocks suitable for the purpose (cf. p. 531).

Rhododendrons and Azaleas. 144 varieties of grafted Rhododendrons are being grown at the Station this year, and 30 of the best varieties have been selected for seeding, in order to ascertain their gametic composition, with a view to future experiments. Special attention has been given to the recently introduced "Pink Pearl," a new break in Rhododendrons, much superior to other varieties in size of flowers and general vigour. It is possible that this hybrid, when selfed, may segregate some useful novelties.

An interesting yellow variety of *Rhododendron* has recently appeared here amongst some hybrid seedlings, which may be the fore-runner of a new race of yellow *Rhododendrons*. An attempt is also being made to secure homozygous lines of some of the best forms of *Azalea sinensis* in different shades of colour.

Berberis. *Berberis* \times *stenophylla*, a garden hybrid of *B. Darwinii* and *B. empetrifolia*, has been seeded here in the open for many years, and a report of the extraordinary variability of the seedlings was made at our first Conference in London 12 years ago (p. 85). At that time Mendel's work was of course quite unknown, and we did not realise then as we do now, that this variability in the second generation is largely Mendelian segregation. Professor De Vries was the first to recognise it, for early in 1900 he wrote to me asking if the *Berberis* hybrids exhibited at the Conference followed Mendel's law. Ever since that time I have tried to self *B. x stenophylla* in all kinds of ways, but so far have failed. Yet, every year it sets quite freely in the open. Dr Shull has suggested to me that the plant is probably self-sterile with its own pollen, and that the seeds produced in the open are the results of pollination by *B. Darwinii*. It may be so, and yet the results obtained from the open flowers seem more likely to have come from self-pollination. Hitherto I have refrained from publishing the *Berberis* data in full, though they provide a particularly interesting illustration of Mendelian segregation, simply because I could not be certain about the precise parentage of the hybrids either in F_2 or F_3 . It must also be remembered that only a single plant of F_1 has so far as I know ever been raised, and that was from a natural cross in a garden. I have failed to repeat the cross after many trials.

At the Station we have some 2500 plants of F_2 and F_3 of the cross, raised from open flowers, and amongst these have appeared a number of valuable garden forms, which clearly have arisen by segregation and re-combination of the characters of the original species *B. Darwinii* and *B. empetrifolia*. Perhaps the best of these forms is one which has the orange-coloured flowers of *B. Darwinii* combined with the graceful, drooping habit of the F_1 hybrid *B. x stenophylla*. Curiously enough this F_2 form is much more vigorous in habit than the F_1 hybrid, and flowers about 10 days later (cf. p. 457).

Hollies. A large number of berries gathered from different varieties of hollies with variegated leaves, have been sown and have given some rather curious results. So far, all those varieties with gold and silver *margined* leaves germinate freely with *yellow* cotyledons, and then perish, producing no adult plants.

On the other hand those varieties with gold and silver *blotched* leaves, germinate with green cotyledons, and grow up into adult plants with green leaves like the common holly. No doubt Professor Baur will be able to throw some light on this curious fact. One difficulty which occurs to me is that the female variegated hollies concerned, must almost certainly have been fertilised by common green males, unless apogamy took place.

To test this matter further, an isolated breeding plot of 14 female hollies with one variety of male has been planted for seed.

The well-known variety of Holly, known as "Golden Queen" is, curiously enough, a male, but this year a single small berry containing only a single seed, has been observed on this variety. If this seed germinates it will be interesting to see what it produces.

Forest Trees. A number of individual trees of straight growing Oaks, true silver-barked Birches, erect-growing Hollies, English Yews, and white-thorn Quicks for hedges have been selected, and isolated as far as possible, from which it is hoped to raise homozygous lines, in order to prevent the large wastage now existent in nurseries where mixed seedlings are grown. In most of these crops I have observed certain beds, in which quite 50% of the plants were either useless and had to be destroyed, or what was almost as bad, had to be transplanted and grown on for several years before they became saleable. If uniform seedlings of these crops could be obtained by the nurseryman the crop would be realised in a much shorter time, it would be much heavier, and would give more satisfaction to the planter.

Fruit Trees. A large number of trees of Apples, Pears, Plums and Cherries have been grown at the Station, and from these, 35 varieties were selected for seeding, as a preliminary experiment. Altogether 157 branches were bagged, consisting of 119 Apples, 16 Pears, 16 Plums, and 6 Cherries. Owing to self-sterility, only a few positive results have been obtained, notwithstanding that most of the flowers were carefully hand-fertilised.

In Apples the only results were 1 medium sized fruit of "Irish Peach" (destroyed by caterpillars), 2 large fruits of "Foster's Seedling," and 2 large fruits of "Lord Grosvenor," each containing apparently good seeds. In Pears the only results were 6 large fruits of "Hessel" containing apparently good seeds, and 3 medium-sized fruits of "Doyenné du Comice" (destroyed by caterpillars). The Plums gave much better results, and the following full-sized fruits containing apparently good seeds, have been gathered, viz.: 6 The Czar, 2 Pond's

Seedling, 55 Victoria; the only variety that failed being "River's Early Prolific."

A number of seeds of "Boskoop Giant" and "Victoria" Black Currants, "Ruby Castle" Red Currants, and "Royal Sovereign" Strawberries have also been gathered, these varieties being apparently fully self-fertile even without hand-fertilisation.

Next year we hope to continue these experiments on a larger scale, the object being to ascertain the gametic constitution of our best garden fruits with a view to future crossings, which it is hoped may give improved varieties.

Mangel-Wurzel. The value of a crop of mangolds depends mainly on the weight of roots grown per acre, the interesting question of the amount of dry matter and feeding qualities in the root being generally regarded as a secondary consideration. According to our experience, in the best cultures, the weight per acre is determined very largely by the shape of the individual root, and the optimum shape appears to be that of an elongated globe, usually known in England as the "Monarch" type. The "Long Red," "Gatepost" and the "Tankard" shapes do not weigh so well as the elongated globe, nor do the ordinary round and flat globes. The "Monarch" type does not however, even in the best of stocks, breed absolutely true. Thus in 2 acres grown here last year there were approximately 70% of the true "Monarch" type, 15% of round globes, 5% of flat globes, 5% of Tankards, 5% of Gateposts and no long reds. In order to secure a homozygous line of Monarchs, 25 selected roots were planted out this spring, their flowers have been carefully bagged and self-fertilised, and it is hoped that some of these will breed true and give the required homozygous line. So far, the seeds seem to have set in the bags fairly well, though apparently not so well as those in the open. Another source of waste in a crop of Mangolds is the frequent appearance of annual roots, which run to seed the first year and are consequently worthless. Professor Bateson has suggested that these annuals may be recessive forms thrown by certain impure dominants amongst the biennials. The varying numbers thrown by different stocks being due to the variable numbers of pure and impure dominants. This may well be so, for I observe that in 20 different stocks of Mangolds, grown for trial and comparison at the Station this year, 9 of them threw no "runners" at all, while others varied from 26 "runners" per acre to as many as 780 "runners" per acre.

To test the matter some of the "runners" have been bagged and

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selfed, and if this view is correct, all the roots grown from them should "run" to seed. On the other hand some of the 25 pure lines noted above should throw no runners at all, being homozygous in that respect, while others should throw runners at the rate of 25%, being heterozygous in that respect.

An interesting problem for the future is a projected attempt to raise a new variety of Mangel with the "Monarch" shape, and the extra dry matter of the white fleshed "Long Red" or the feeding qualities of the yellow fleshed "Tankard." At present however these distinct qualities seem to be incompatible with one another, and it may be impossible to obtain such a combination.

Swede Turnips. 40 roots of two varieties, purple-top and green-top Swede Turnips have been seeded in order to raise homozygous lines of each. Both varieties appear to be fully self-fertile.

Drumhead Cabbage. The value of a crop of Drumhead Ox Cabbages depends on the weight of food stuff produced per acre, and under good culture, this rests mainly on the size and hardness of head of individual plants. A further important consideration is that as the plants must be autumn sown to get the best results, the young plants must be sufficiently hardy in constitution to withstand a severe winter in the seed-beds. Four selected varieties have been tested at the Station this season, and the best one undoubtedly is a local variety that has been grown here for many years under the old method of mass selection. This variety is known under the name of Blue Drumhead, and is so called because the leaves contain a good deal of purple sap, and also carry a peculiar glaucous bloom of a waxy nature. In this respect it differs considerably from the ordinary green Drumheads, and it has the further advantage of producing but few runners in the seed-beds, when sown at the normal time. An acre of this variety was planted out last year and seemed fairly true to type as regards blueness and hardness, though it varied considerably in size and hardness of head; about 5% were green with white ribs and veins like the ordinary Drumhead, about 5% never turned in properly, about 1% were red pickling Cabbages, a few odd plants were purple-leaved kales, while a single plant was a curious combination of a Cabbage and a Brussels Sprouts.

25 individual plants of these were selected and planted out last autumn, the flowers carefully bagged and hand-fertilised this summer, and it is hoped that amongst them will be found a homozygous line that will throw no "rogues."

Unfortunately, there seems to be a high degree of self-sterility

amongst these Cabbages: thus one plant produced only 2 good seeds, others from 6—20 each, others 50—100 each, one plant gave 300, and another 550 seeds.

This compares unfavourably with results obtained from selfed Swede Turnips, which being fully self-fertile, have produced from 1000 to 2000 seeds each.

The question of running to seed is perhaps more important in Cabbages than in Mangels. In Cabbages however the question is apparently more complicated by the influence of conditions, *e.g.* early sowing. There is no doubt however that different stocks of Cabbages give different proportions of "runners" even when sown at the same time and under similar conditions. For instance, in the 4 stocks sown here at the same time last autumn, the first gave 290, the second 2223, the third 5892 and the fourth 12,157 runners per acre in the seed beds. How far these figures would have been affected had the seed been sown a month earlier is problematical. This year, a series of sowings have been made twice a week through July and August to further test this important matter.

Poultry. A number of chickens of White Leghorns and White Wyandottes, bred from two distinct "200 egg" strains, have been reared, and an attempt will be made to raise from them homozygous lines that will maintain this standard of egg-production. To do this in the case of the Wyandotte, it may possibly be necessary to eliminate the broody instinct, which in my previous experiments appeared to behave as a Mendelian dominant character in Buff Cochins. In such a case, it will be interesting to see whether the coloured egg disappears with the broody instinct (*cf.* pp. 461 and 468).

Pigeons. We have this year taken up the breeding of the Homing or Racing pigeon at the Station and have found it a most interesting study. The principal characters that go to make an efficient racing pigeon in good training, appear to be mainly mental and temperamental. The rapid development of the modern homer in recent years seems to have been due to the rigid selection or natural weeding out process, which takes place in the best lofts. The system being that only those birds that have the intelligence and determination to return home quickly from long distances, are bred from. The "wasters" either succumbing by the way, or are trapped and bred from by second-rate fanciers. Notwithstanding this rigid selection of breeding stock, the best birds still throw "wasters," and our object is to attempt to raise homozygous lines which will throw no "wasters." Two distinct strains

have been bred from this year, a pure-breeding blue and a pure-breeding red strain; a number of "squeakers" have been reared, trained and raced with a local Flying Club this summer (cf. p. 458).

It is interesting to note that feeble-mindedness seems to be a recessive character in pigeons, as well as in Man.

Rabbits. In the whole range of fancy live stock, perhaps the most difficult animal to breed is a Champion Dutch Rabbit. It is quite an ordinary experience with Dutch fanciers to breed 1000 animals of the best pedigree, without obtaining a Champion (fig. 164). One of the reasons for this is undoubtedly that the model markings required in a Champion winner are fluctuating variations which are not germinal. At the same time my experiments show that at least 25% of the "wasters," i.e. the spotted forms, can be eliminated. The "Dutch" winner has about equal proportions of coloured and white fur arranged in a regular pattern. The offspring of winners however vary considerably in these proportions of coloured and white fur. If 5 be taken to represent equal proportions of coloured and white, and 6, 7, 8 and 9 represent increasing excess of coloured over white, then 9 will be almost self-coloured. If 4, 3, 2 and 1 represent increasing excess of white over coloured, then 1 will be almost white (figs. 96 and 161). (See pp. 260 and 460.)

So far as my experiments have gone, 5×5 gives 1, 2, 3, 5, 6, 7 and 8, the types 4 and 9 being absent. Now 1, 2 and 3 breed true to 1, 2 and 3, giving no higher form. Consequently 5, 6, 7 and 8 being dominant to 1, 2 and 3, pure dominants can be raised carrying no low numbers. Steps are being taken to raise these homozygous lines that will not throw the spotted wasters. Professor Punnett of Cambridge has recently been good enough to send me a pair of chocolate rabbits, with the object of introducing this new and striking colour into the Dutch breed.

Horses. A study of the General Stud Book and Racing Calendar has revealed the existence of several Thoroughbred mares and stallions, which when bred together give nothing but steeplechasers (see p. 412).

In view of this fortunate find of what is apparently a homozygous line of 'chasers, steps are being taken to purchase mares and stallions, the offspring of this line, for experimental breeding. Thanks to the keen interest and kind generosity of Captain Part of the 21st Lancers, it has been possible to put these Mendelian experiments into operation this season. The experiments will be carried out partly at this Station and partly at Captain Part's Stud in Hertfordshire. The Board of Agriculture and Fisheries, London, have detailed their Superintending

Inspector, Mr F. W. Carter, to watch and assist the experiments on their behalf. It is hoped that these experiments may help to solve the practical problem of the making of a homozygous hunter.

Experience suggests that the hereditary factors concerned in the making of a hunter or 'chaser, represent mental and temperamental qualities rather than purely physical characters, as is usually supposed.

In the hunter for example, a perfect physical conformation is useless without the "jumping temperament," and the possession of courage in a trial of endurance, is often a greater asset than a powerful physique.

This particular case provides an illustration of some unexpected possibilities in the application of the principles of Genetics to practical problems. In this case, like many others, we have at present no knowledge whatever of the Mendelian units which go to make a 'chaser or a hunter. All we know is that certain matings produce such horses, while others do not, even with the best possible training.

There may be many gametic units concerned or there may be but one.

The important point is, that notwithstanding our present ignorance of the precise gametic units or combination of units, that go to make the hunter or 'chaser zygote, we can still proceed to apply the *principles* of Genetics to the practical problem of hunter-breeding with some hopes of success. In such cases, the practical application is of necessity in advance of present knowledge, and therefore involves true experimental research.

Man. Pedigrees of local families, and individual observations of the colour of the eyes, hair and skin of the local population, are being recorded at the Station. The results so far obtained, show clearly that Mendelian segregation is taking place in Man, much as it is in other animals and plants. Segregation is most apparent in such characters as brown and blue eyes, brown and red hair, dark and fair skin, pale and coloured complexion, non-musical and musical temperaments, which broadly speaking, appear to behave as Mendelian dominants and recessives, respectively. Other characters, including mental and moral qualities, are also under investigation.

With regard to the application of the principles of Genetics to practical human problems, there is no doubt that the human race can be improved, and made more efficient physically, mentally and morally by the application of the principles of Genetics, equally with domesticated animals and cultivated plants, provided always, that Man is willing to take the necessary action.

XXIX

MENDELIAN HEREDITY IN MAN¹

During the last ten years the Mendelian principles of heredity have been applied with remarkable success to various characters in many kinds of plants and animals. These Mendelian experiments have given rise to the new science of Genetics. In the absence of controlled matings, the analytical methods of Genetics are obviously difficult to apply to Man, and for his analyses the student has to rely on observations of the results of random matings. In spite of this heavy handicap, and notwithstanding the almost equally serious drawback of having to deal with small families, considerable progress has been made, and there is no doubt that at the present time we have sufficient positive evidence to demonstrate the working of Mendelian heredity in Man, and to encourage students to pursue their investigations over a wider field. A large amount of work has been done recently in the way of collecting pedigrees from different sources, illustrating the inheritance of various characters in Man, and in certain cases where the pedigrees have been critically analysed in the light of the Mendelian principles, some valuable results have been obtained. The results obtained by Farabee (10), Nettleship (21), Davenport (3—7), Gossage (12), Mudge (19), Drinkwater (9), Goddard (11), Salaman (23), and Jordan (16), provide good illustrations of the value of this method of work.

During the past ten years the writer has adopted the somewhat different method of making personal observations on the individual characters of the parents and children living in and about the village of Burbage, Leicestershire. (This district consists of an industrial village with outlying hamlets, altogether comprising a population of about 3000 persons.) In all Mendelian researches, whether in plants, animals or Man, the advantages of personal observation seem far to outweigh the disadvantages of small numbers in a limited area.

In view of the various characters touched upon in this paper, it is, of course, impossible to attempt to deal with any single character exhaustively, consequently the paper can only be regarded as an introductory sketch. Further details may be found in the literature cited.

¹ An address delivered before the Eugenics Education Society, London, Nov. 16, 1911, and reprinted from *The Eugenics Review*, iv. pp. 1-25 (1912).

Eye-Colour.

Human eye-colour depends mainly on the colour of the iris, which is largely determined by the presence or absence of two distinct layers of pigment. In the true blue eye only one of these pigmentary layers is visibly present, the posterior purple pigment of the choroid, which, being reflected through the fibrous structure of the iris produces the blue colour. In the absence or partial absence of this pigment the eye appears to be "pink" as in albinos. In the ordinary brown eye two layers of pigment are present, for in addition to the posterior purple layer there is also an anterior brown layer, in front of the iris.

In order to distinguish eyes with two layers from eyes with one layer of visible pigment, the writer (14) in 1907 called the one Duplex and the other Simplex, and further found that these two types of eyes in their genetics follow the ordinary Mendelian rules, Duplex being dominant and Simplex recessive. Or applying the presence and absence method—presence of the brown front layer is dominant to its absence (see p. 272).

Simplex eyes may be any shade of blue or grey according to the fineness or coarseness of the structure of the iris, consequently baby-blue eyes may develop into adult grey eyes. Duplex eyes may be any colour from "black" (very dark brown) to "blue," according to the amount of brown pigment present on the front of the iris. If the amount of brown pigment is small such Duplex eyes may be easily mistaken for Simplex when viewed at a short distance or in a bad light. A close lateral inspection in a good light will, however, generally determine the presence or absence of visible pigment in front of the iris, without the assistance of a lens.

An attempt to differentiate the various grades of blue and grey Simplex eyes has so far proved unsuccessful owing partly to their apparent continuity and partly to their changes with age. An attempt to differentiate the various grades of Duplex eyes has been more successful, though experience shows that great caution is necessary to avoid the many pitfalls that exist even for the wary.

In 1907 the writer suggested that Duplex eyes might be classified into three definite patterns, Self, Ringed, and Spotted.

In the Self pattern, the brown pigment is distributed over the entire surface of the iris, the rays being pigmented to the periphery. To this class belong eyes generally known as "black," dark brown, brown, red-brown, yellow-brown, green-brown and green, according to the density

of the melanic pigment covering the front of the iris, and possibly also in some cases to the existence of a distinct yellow or orange pigment (lipochrome) diffused with the brown melanin.

In the Ringed pattern the brown pigment is confined to a ringed area round the pupil, leaving a solid blue or grey rim round the periphery. In some cases the ring of pigment is clearly defined and narrow, while in others it is irregular in outline and broader with fimbriated rays. To this class belong eyes generally known as grey-brown, dark grey, grey, grey-green, and blue-green.

In the Spotted pattern the inner ring is altogether absent or broken up into discrete patches, blotches or spots. These spots are usually irregular in size, number and distribution over the blue or grey ground colour. Similar spots are to be found in certain eyes of the Self and Ringed patterns, but these are on a lighter duplex ground, while those of the true spotted pattern are on a simplex ground colour.

With regard to the genetics of these Duplex patterns, so far as adults are concerned the Self seems to behave as a dominant to the Ringed which is recessive, following the ordinary Mendelian rules. In the case of juveniles, however, great care is necessary, because since 1905 I have found several cases in which the Ringed pattern has developed into the Self pattern with age. The Spotted pattern is rather rare in my material, but, so far as the evidence goes, it appears to behave as a dominant both to the Self and Ringed patterns, suggesting that it may be due to the presence of an inhibitor. It is interesting to note the close analogy between the genetics of the Self, Ringed and Spotted patterns of eyes in Man, and the Self, Dutch and English patterns of coat colour in rabbits.

Dr C. B. Davenport and Mrs Davenport (3), of the Carnegie Institution of Washington (who discovered the Mendelian nature of eye-colour almost simultaneously with the writer (13)), make three grades of eye-colours, brown, grey and blue in the order of their dominance. This is certainly a more simple interpretation of the facts which, though broadly in agreement with the writer's scheme, differs from it in one important particular, inasmuch as it leaves untouched the peculiar problem of the Spotted eye.

In following up their scheme, Davenport and Davenport find that the darker grade of eye-colour is always dominant to the lighter grade, so that no children have darker eyes than the darker parent. In order to test this broad generalisation of the "Non-transgressibility of the

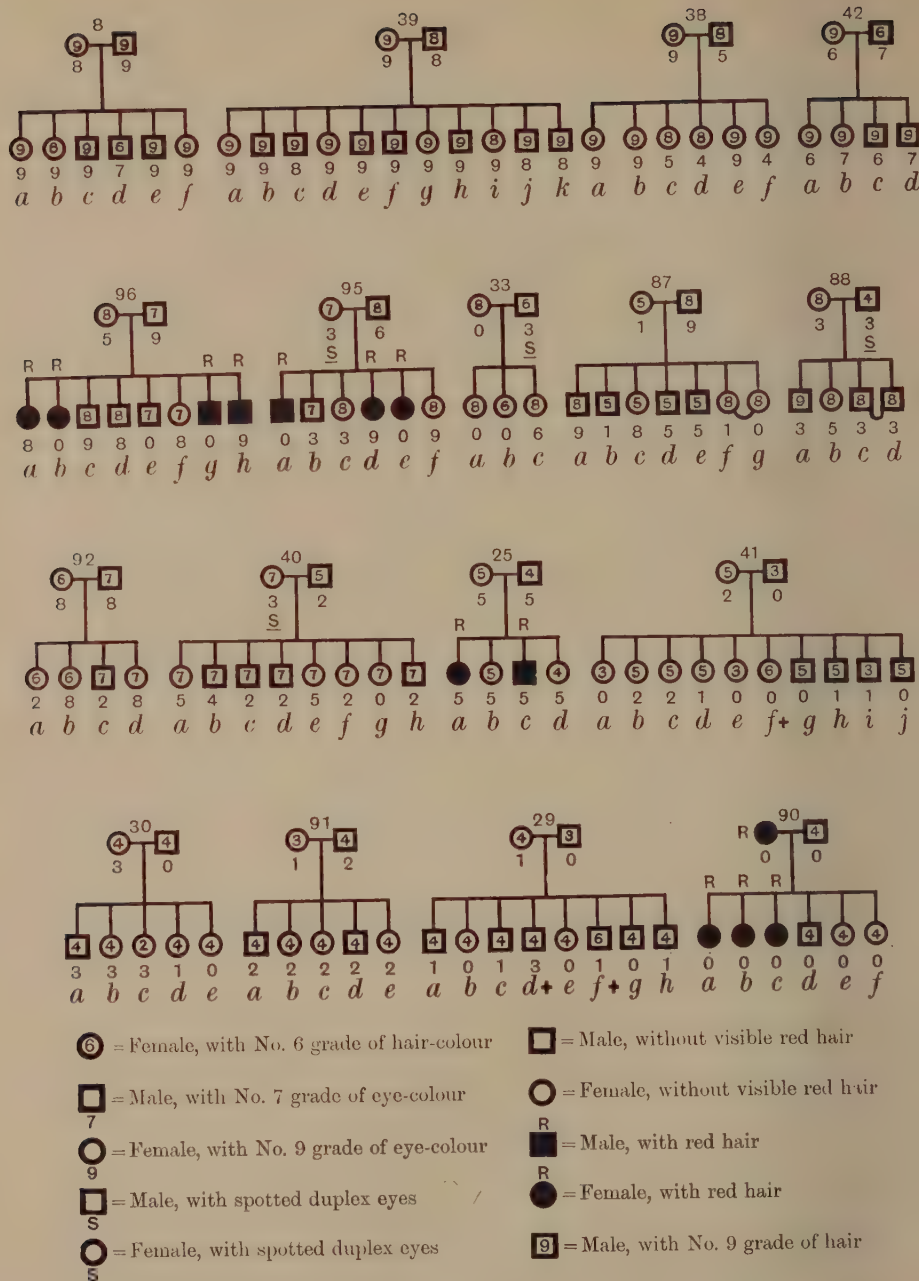


Fig. 125. Eye-colours and Hair-colours in the Burbage Families.

Upper Limit," I have attempted to grade the eye-colour shades in some of the Burbage families from 0—10 according to the amount of brown pigment present on the iris.

Thus 0 represents the blue or grey Simplex eye with no brown pigment: 1, 2 and 3 are blue or grey Duplex eyes of the Spotted or Ringed patterns: 4 is a dark grey, grey-green, or grey-brown, a broadly ringed pattern: 5, 6, 7, 8 and 9 are Self patterns varying in shade from light green to dark brown, and 10 represents "black" eyes (really a black-brown) like those found in some negroes, but not met with in the Burbage families.

According to this method a numerical grading of the brown pigment is obtained by the two-fold consideration of distribution and density, the shade of the blue or grey ground-colour being ignored as far as possible.

The families in fig. 125 have been worked out on this system, the figures *underneath* each square and circle representing the estimated grade of brown pigmentation in the eyes.

The pedigrees, on the whole, tend to confirm the Davenports' generalisation, the striking exceptions being the cases of Spotted Duplex eyes which, notwithstanding their lowness of grade, give offspring of a higher grade than either parent (see families 40, 88, 95 and 33). The single case of family 29*d*, where the higher parental grade 1 gives a solitary instance of grade 3 is at present inexplicable, as both the 1 and 3 grades concerned are apparently of the ordinary ringed pattern. Family 25 is interesting as a case of an apparently pure-breeding 5 grade, and the youngest daughter of this family (25*d*) is a specific case of the change with age from a Ringed to a Self Duplex: in 1905 her eyes were classed as Ringed Duplex representing grade 3, whereas in 1911 they were Self Duplex representing grade 5. The increase of pigment in this case was two-fold, representing an increase of 1 grade in distribution and 1 grade in density.

Hair-Colour.

Davenport and Davenport (5) have shown that two distinct pigments may be present in human hair, a granular brown melanin and a diffused red lipochrome. Somatic interaction between these two pigments gives complicated results, so that it will be convenient to deal with them separately.

Brown Pigment.

According to the Davenports, human hair with brown pigment varies in shade from black to light yellow according to the amount of brown pigment present. Unlike similar hair-colours in rabbits, mice, and guinea-pigs, which experiments have shown to be discontinuous, the shades of human hair appear to be continuous. The Davenports, however, conclude that in all cases the higher and darker grade is dominant to the lower and lighter grade, which is recessive. Consequently, children in no case have darker hair than their darker parent, being another illustration of the Davenports' generalisation of the "Non-transgressibility of the Upper Limit." In order to test this generalisation with my own material, I have attempted to grade the brown hair-colours of some of the Burbage families from 0—10, grade 0 representing white "albino" hair with no pigment, and grade 10 representing jet black hair with no trace of brown. Neither of these grades has yet been found in my material. Grades 1 and 2 represent silvery cream and pale yellow hair, so far only met with in juveniles. Grades 3 and 4 represent yellow and yellow-brown hair: grades 5 and 6 represent medium brown and deep brown hair: while grades 7, 8, and 9 represent dark-brown, black-brown and ordinary "black" hair respectively.

A serious difficulty however arises, a difficulty which at one time I feared would be insurmountable, and that is the frequent and considerable changes of colour that human hair undergoes in the progress of development and decay during the life of the individual. These changes of colour from birth to death appear to be very variable in different individuals. In many individuals the true adult hair-colour of the head can only be observed during a brief period of time, and often before the children reach the adult stage the parents are already grey.

In view of these facts any first-hand investigation of the inheritance of human hair-colour by comparison of parents with children would appear to be extremely difficult, if not altogether impracticable. Fortunately, however, the writer has found that the colour of the eye-lashes at practically any age seems to be a fairly reliable index to the adult head-hair. Generally speaking, one finds that in very young children the pigment of the eye-lashes develops much more quickly than that of the eye-brows and head hair, and with few exceptions the colour of the eye-lashes in juveniles may be taken as a fairly approximate index of what the adult hair will be. Similarly in old people with grey hair, the colour of the eye-lashes will generally give one a fair idea of what the adult hair was like.

It is true that a few cases have been observed in normal adults where the eye-lashes are darker or lighter than the hair of the head and eye-brows, but generally the eye-lashes seem to provide a fairly reliable index of the mature head hair-colour at all ages.

The brown hair-colour gradings in fig. 125 are all based on the colour of the eye-lashes in both parents and children, the grade numbers being inserted *within* the squares and circles. So far as these observations go, they seem to confirm the Davenports' generalisation that no children are darker than the darker parent. The slight exceptions are seen in family 41, where a single child apparently oversteps the higher parental grade by 1 point, and in family 29 one child is apparently 2 grades darker than the darker parent. It will be noted that it was in this family that an elder brother was similarly exceptional in eye-colour.

Red Pigment.

In Man red hair exists in many continuous shades from a light yellow-red to a dark chocolate-red. The Davenports provisionally suggest that the red or reddish-yellow pigment may exist in different dilutions and intensities, and also apparently, with or without the sepia brown pigment. This may possibly be so, but so far as my observations go a more simple scheme seems to explain the facts equally well. All the various shades of red hair known to me in humans, can, I think, be accounted for on the basis of the somatic association of a uniform red or orange pigment with each of the grades of brown pigment noted above. Thus if N1—N9 represent the various grades of the brown hair from cream-coloured to "black" and R a uniform red or orange pigment, then :—

N1 + R = Silvery Cream with Red producing	<i>Pale red</i>
N2 + R = Pale Yellow " " "	<i>Light red</i>
N3 + R = Yellow " " "	<i>Fiery red</i>
N4 + R = Yellow-brown " " "	<i>Sandy red</i>
N5 + R = Medium brown " " "	<i>Auburn red</i>
N6 + R = Deep brown " " "	<i>Chestnut red</i>
N7 + R = Dark brown " " "	<i>Chocolate red</i>
N8 + R = Black-brown " " "	<i>Black-brown</i> (Red masked)
N9 + R = "Black" " " "	<i>"Black"</i> (Red masked)

If the above interpretation of the facts is correct there is apparently no need to presume that the red pigment is found alone in the complete absence of the brown pigment. Indeed I imagine that such a presumption would be not only exceedingly difficult to establish by

observation, but would also involve the more frequent occurrence of albinos in red-haired families than actually observed. Nor does it seem necessary to presume that the red pigment itself exists in various intensities and dilutions when its associations with the various grades of brown pigment appear to provide all the sorts of red observed.

With regard to the genetics of red hair in Man, in 1908 the writer (15) published a brief account of his investigations in the Burbage families and at that time pointed out that Red hair seemed to behave as a Mendelian recessive to Brown which appeared to be dominant. These conclusions were based on the following observations:—

First, when both parents had red hair, all the children were red.

Second, when both parents had brown hair, *either* all the children were brown, *or* most of them were brown and a few were red.

Third, when one parent was brown and the other red, *either* all the children were brown, or about one-half were brown and one-half were red (see p. 289).

Since 1908 further investigations have been made which not only confirm and extend the previous observations but demonstrate clearly that in all the families where red-haired children appear, the brown-haired parents are without exception descended from families containing red-haired children. While, on the other hand, in those families in which red-haired children do not appear at all, the brown-haired parents are in many cases descended from families which have not thrown reds. All these observations seem to point to the recessive nature of red hair and the dominance of brown.

The adoption of the "presence and absence" method in genetics has, however, led us to regard such a character as red hair as hypostatic (rather than recessive) to brown hair, which is epistatic (rather than dominant). The Davenport's demonstration of the fact that the red pigment in human hair is a lipochrome distinct in its nature from the brown pigment, which is a melanin, goes far to confirm this idea. It would appear, therefore, that we might now regard the red pigment as due to the presence of a distinct unit-factor dominant to its absence.

On this view, presence of the factor for red should give visible red hair (except where it is masked by dark melanin as shown above), while absence of the factor for red should give hair with no traces of red. If (R) represents presence of red and (r) its absence, then all individuals should be gametically (RR), (Rr), or (rr). Red-haired individuals should be either (RR) or (Rr), while brown-haired individuals should be all (rr), except as aforesaid in those cases where the grades of brown are so dark

(8, 9 and 10) as to mask the red which may be present though invisible.

In order, if possible, to avoid the masking complication it seems necessary to consider those brown-haired individuals where there is presumably no masking of the red pigment, namely, in the lighter grades of brown 1—6. These low grade browns should be gametically (rr), and, therefore, cannot be expected to give red-haired children when mated together. Similarly these low grade browns (rr) when mated with reds (RR) or (Rr) may be expected to give *either* all reds $(RR) \times (rr) = (Rr)$, *or* one-half reds and one-half browns

$$(Rr) \times (rr) = 1 (Rr) + 1 (rr).$$

While two red-haired parents (RR) or (Rr) should give *either* all red-haired children $(RR) \times (RR) = (RR)$, $(RR) \times (Rr) = 1 (RR) + 1 (Rr)$, *or* about 3 reds to 1 brown $(Rr) \times (Rr) = 1 (RR) + 2 (Rr) + 1 (rr)$.

In no case, however, do these expected results accord with the observed facts, for:—

First, the low grade browns *do*, in many cases, give reds when mated together.

Second, the low grade browns mated with reds in no case give all reds, so far as observed.

Third, two red-haired parents in no case give children with brown hair, so far as known.

The question arises, therefore, what is the explanation of the whole matter? So far as one can see, the case seems to admit of only one explanation, which though simple in itself, may present certain difficulties to the orthodox Mendelian. The suggested explanation is, that in order to have visible red in the hair two doses of the factor (R) are necessary (RR), and that in the presence of one dose (Rr) the red colour is either not developed at all, or only developed so slightly as to be masked by the melanin, and therefore invisible.

On this scheme two brown-haired parents (rr) would give *all* brown-haired children (rr). A brown (Rr) mated with a brown (rr) would give all browns $(Rr) + (rr)$. Two brown (Rr) would give about one-quarter reds 1 (RR) and three-fourths brown 2 (Rr) + 1 (rr), giving the novel and heterodox Mendelian ratio of 1 *Dominant* to 3 *Recessive*.

Similarly brown (rr) mated with red (RR) would give *all* brown (Rr). The brown (Rr) mated with the red (RR) would give about equal numbers of red (RR) and brown (Rr). While two red (RR) parents would give, of course, all red (RR) children.

On this scheme all the expected results seem to be in accordance with the observed facts. This suggested solution of the puzzling problem of the inheritance of red hair introduces a novel Mendelian ratio, which, if confirmed and extended to other characters in plants and animals, would be of considerable importance, inasmuch as it might go far to explain several well-known cases of apparent reversal of dominance in plants and animals which have so far remained inexplicable.

At the same time this suggested solution is advanced with considerable reluctance, because the writer feels that it would have been more acceptable, had it been first found in some cultivated plant or domesticated animal, where the matter could have been quickly and easily put to the test by conclusive experiments. The only excuse for putting it forward in the case of a human character is that no other explanation seems to be available if the "presence and absence" method is adopted.

Skin-Colour in "White" Races.

Davenport and Davenport (6) have recently published an important paper on the "Heredity of Skin Pigmentation in Man," in which the Skin-colours of typical Caucasians are divided into three categories, "Brunet," "Intermediate" and "Blond."

Professor H. E. Jordan, of the University of Virginia (17), in his microscopical studies on the melanin content of human skins, has since demonstrated clearly that in the "Brunet" the melanic pigment granules are more numerous than in the "Blond" skin.

The Davenports have collected numerous data from various sources, with the result that they find that their principle of the "Non-transgressibility of the Upper Limit" seems to apply to these skin-colours much in the same way as in hair and eye-colours. That is to say the higher and darker grade "Brunet" is dominant (epistatic) to the lower and lighter grades "Intermediate" and "Blond," while "Intermediate" skin-colour is dominant (epistatic) to "Blond," which is recessive (hypostatic) to both.

Consequently the children of "Brunet," "Intermediate" and "Blond" parents are in no case darker than the darker parent.

In order to test this generalisation in my material I have attempted to divide the skin-colours in the Burbage families into the three categories, "Brunet," "Intermediate" and "Blond." So far this attempt has not proved at all satisfactory, as there seem to be various

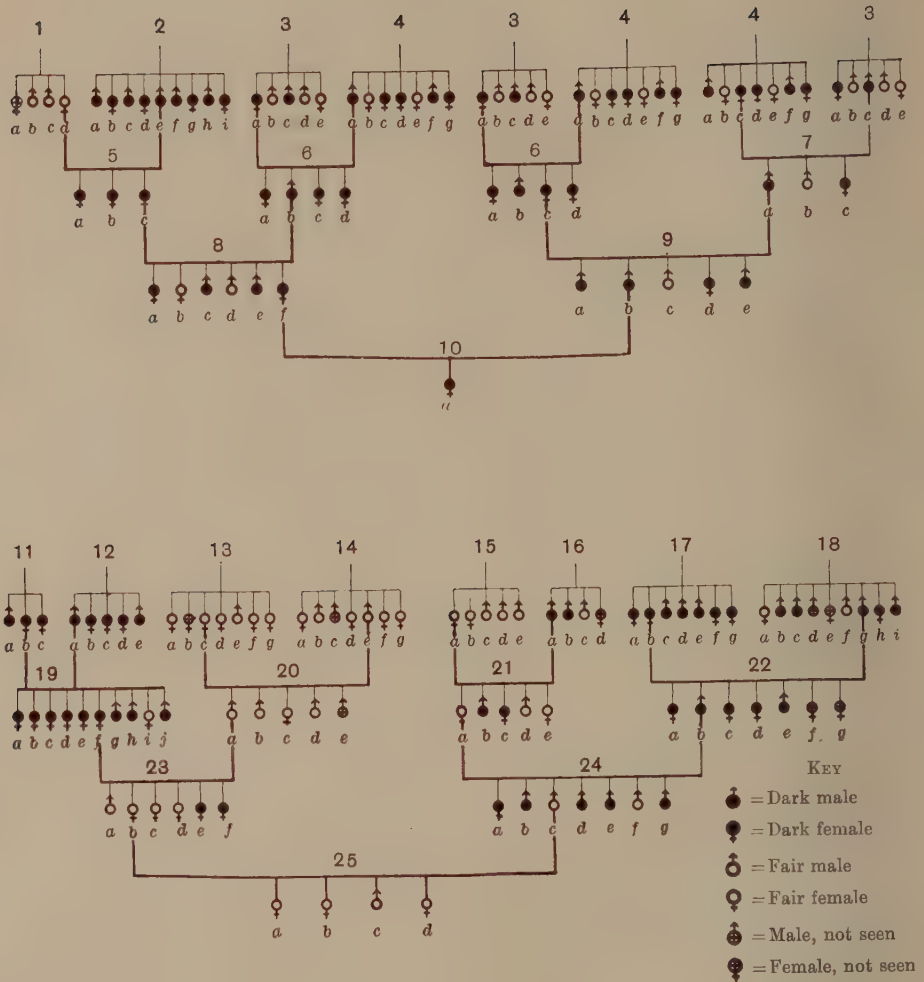


Fig. 126. Skin-colour in the Burbage Families.

grades both of darkness and fairness in different families. A further attempt to divide skin-colours into ten grades as in the hair and eye-colours has not been at all successful owing to the elusive nature of the different shades. At the same time it is evident that in many families there is a definite segregation of dark and fair skins, and in this respect the Davenports' suggestion that the higher and darker grade is dominant to the lower and lighter grade is certainly confirmed so far as my observations go.

The pedigrees in fig. 126 will serve to illustrate the dominance of dark to fair skins, their segregation in the same family, and the apparent purity of the extracted fair individuals.

It should, however, be carefully noted that while the dark individuals in each family may be sensibly uniform in tint, yet in the different families there are different grades of darkness. A similar state of things appears also to exist amongst the fair individuals. It is quite possible, therefore, that a certain amount of overlapping might occur with these two categories "Dark" and "Fair" in certain pedigrees, though in the above pedigrees the two categories are quite distinct.

For instance, the dark members of families 19 and 22 are decidedly darker than the dark members of families 3 and 4, while the fair members of families 13, 14 and 20 are certainly fairer than the fair members of families 3, 4 and 8, yet the segregation of the dark and fair in families 3, 4 and 8 is quite palpable and clear cut.

Complexion Colour.

While investigating the question of skin-colour in the Burbage families, the writer has found his observations somewhat complicated by the different colourings of the complexion. Thus both dark and fair skins may be either pale or coloured. These differences in complexion colour appear to depend on the thickness of the skin, pale skins being thick and coloured skins thin. Generally speaking, a dark, pale skin makes a sallow or muddy complexion: a fair, pale skin a clear complexion: a dark, coloured skin a ruddy complexion: and a fair, coloured skin a florid complexion.

So far as my observations go, the pale thick skin seems to behave as a Mendelian dominant to the coloured thin skin which is recessive. At the same time, owing to the scarcity of coloured by coloured matings the evidence is not yet sufficient to establish the statement fully. The

few families with two coloured parents have so far given all the children with coloured complexions. Cases of two pale parents giving either all pale, or a few coloured, are quite numerous, as are the cases of pale by coloured giving either all pale or about one-half with coloured complexions.

It is possible, moreover, that coloured complexions in adults really consist of two distinct classes, viz.: "red," where the colouring extends over the whole of the face and neck, and "fresh" where the colouring is confined to a definite area in the cheeks. The precise relationship between these two classes is not yet known.

The above notes illustrate once more that the apparently simple question of the dark and fair colouring in "white" races is really a most intricate and complicated problem, which cannot be satisfactorily dealt with by the ordinary methods of the anthropologist. Sufficient evidence, however, has been obtained to show that, notwithstanding the apparently continuous nature of the pigmentation of the eyes, hair and skin of "white" races, the discrete Mendelian factors are at work in Man as well as in domesticated animals and cultivated plants.

Further investigation will no doubt determine many other Mendelian factors which are concerned in the heredity of colouring in Man, and also the interesting question as to how far these different factors behave as independent units, and what amount of association exists between them in the production of the visible soma of the two sexes.

With regard to the possibility of sex limitation or linkage, it may be interesting to note that in the pigmentation characters so far observed only two families (quite unrelated) have shown any signs of such a phenomenon. Curiously enough in both families the dark hair and skin of the father were apparently transmitted to the daughters only, the sons (with a single exception in one family) having fair hair and skin similar to those of the mother. The numbers (9 males and 10 females), however, are too small to attach much importance to the observation, and both may be merely curious coincidences.

Left-handedness.

The occasional appearance of left-handed individuals among normal right-handed brethren is a familiar fact, and there is a widespread popular belief that the peculiarity is inherited.

An interesting paper by Jordan (16) gives a concise history of the probable causes of left-handedness, together with a number of pedigrees

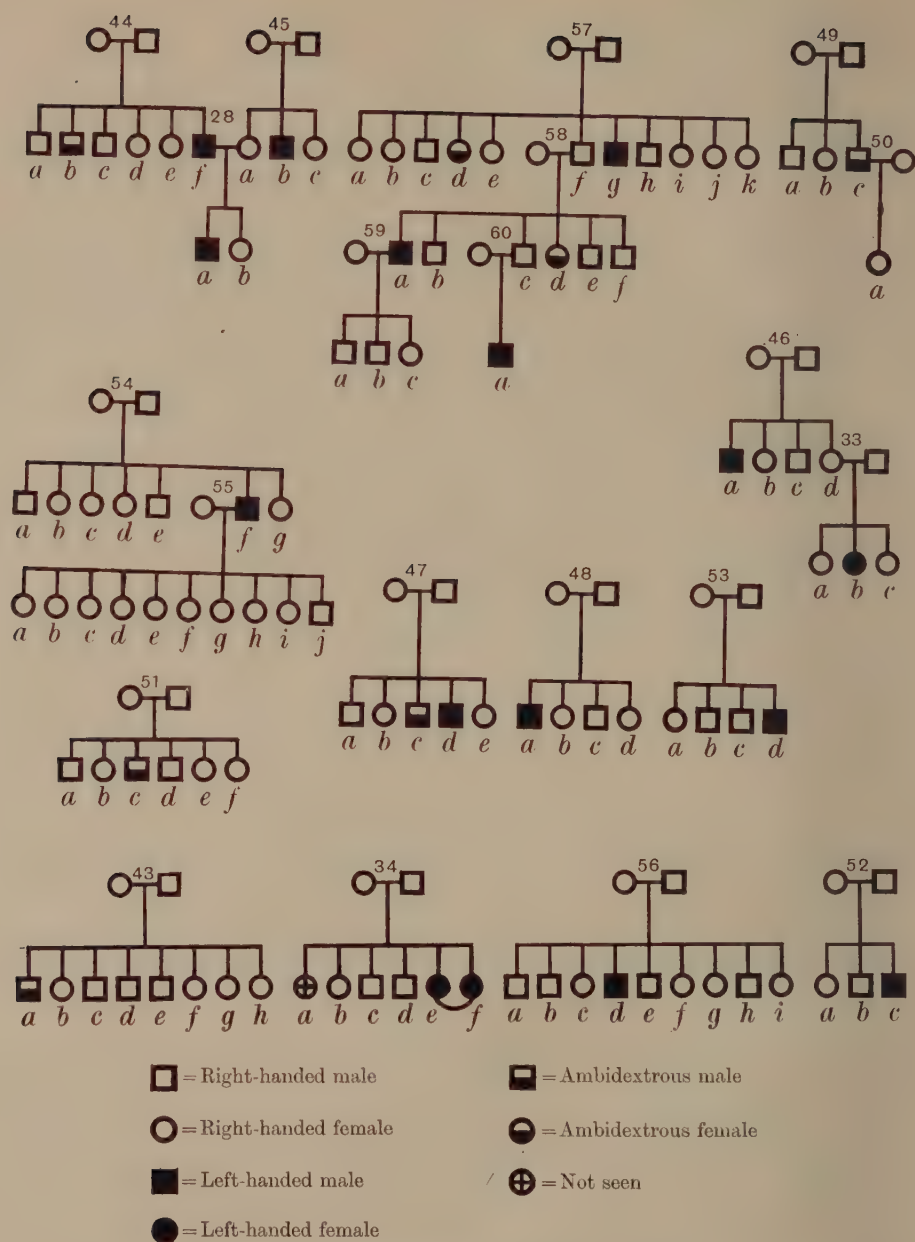


Fig. 127. Left-handedness in the Burbage Families.

which certainly support Jordan's conclusion that left-handedness is hereditary.

Jordan cautiously suggests as a guiding hypothesis, that left-handedness may be a Mendelian character recessive to right-handedness which is dominant, and further, that ambidexterity may possibly represent a condition of imperfect dominance of the right-handed over the left-handed character.

In view of Jordan's paper, the writer has made some investigations with regard to the appearance of left-handedness in the Burbage families.

The pedigrees in fig. 127 illustrate the results so far obtained.

On Jordan's hypothesis that right-handedness is dominant and left-handedness recessive, most of the matings illustrated in fig. 127 would be of the nature of heterozygous right-handed individuals, which should give on the average one-fourth of the children left-handed. Counting the ambidextrous among the right-handed as Jordan suggests (imperfect dominants), and omitting the families with only one child, we get 73 right-handed to 14 left-handed children, a ratio nearer 5 : 1 than the expected 3 : 1. If, however, on the other hand, we regard the ambidextrous as left-handed, we get 66 right-handed to 21 left-handed children, a ratio very near to the expected 3 : 1. Further inquiry into the ambidextrous cases shows that, with the exception of one or two doubtful cases, the congenital bias was undoubtedly to left-handedness, the ambidexterity being apparently acquired as an adaptation to circumstances. In view of this it seems more reasonable to classify these ambidextrous cases as left-handed rather than right-handed.

Jordan's cases of similar parentage, omitting families with only one child, apparently give 21 right-handed to 12 left-handed children, a ratio nearer 2 : 1 than the expected 3 : 1. This, however, may be due to the fact that some of his families were admittedly incomplete, and consequently somewhat smaller than the Burbage families, which are fairly complete. Two left-handed parents have not yet been found in the Burbage families, but Jordan gives two cases in which the two offspring were left-handed in accordance with expectation. Jordan also gives 11 families of left-handed mated with heterozygous right-handed parents giving 24 right-handed and 22 left-handed children, which is in accordance with the expectation of equality. The Burbage families only supply one case of this mating giving one of each kind (family 28).

On the whole the evidence, so far as it goes, seems to favour Jordan's hypothesis that left-handedness in Man is a Mendelian recessive

character, but his idea that ambidexterity is the condition of imperfect dominance of the right-handed over left-handed is not so far confirmed¹.

Hand-Clasp.

All persons naturally clasp their hands in one of two ways, *either*, with the right thumb over the left thumb, in which case it is called a right-handed clasp, *or*, with the left thumb over the right thumb, in which case it is called a left-handed clasp. In practice one finds that certain nervous or self-conscious people when asked to clasp their hands are apt to wander with their thumbs. In such cases the position of the fingers provides an equally accurate index to their hand-clasp, if the fingers of each hand are alternated as they should be when the hand is properly clasped.

The manner of the clasping of the hands—right or left—seems to be congenital, being quite constant in very young children, and one naturally expects to find such a character inherited. The first to draw attention to this matter was apparently Dr Frank E. Lutz, of U.S.A. (18), who, with the assistance of Prof. J. Arthur Thomson, of Aberdeen University, collected data for about 600 individuals. The result was certainly unexpected, inasmuch as neither position bred true, and did not seem to follow the Mendelian or any other system. Thus,

Two right-clasped parents gave 72·5 per cent. right-clasped children.

Two left-clasped parents gave 42·2 per cent. right-clasped children.

While right-clasped mated with left-clasped parents gave about 56 per cent. right-clasped children.

In view of these curious results steps have been taken to investigate the matter in some of the Burbage families. It was thought that a separate study of individual families might throw some light on the question. The pedigrees in fig. 128 will suffice to illustrate the results obtained.

It will be seen that the observations made in the Burbage families give similar results to those collected by Thomson and Lutz. Neither right nor left position breeds true. Right by Right gave 15 rights and 11 lefts, no family giving all rights. Left by Left gave, curiously enough, the same result—15 rights and 11 lefts, no family giving all lefts. Right by Left and Left by Right gave 20 rights and 27 lefts. All the families taken together with all kinds of matings gave 50 rights

¹ In later papers Professor Jordan shows conclusively that left-handedness is a Mendelian recessive character and accepts my view that ambidexterity is usually based on left-handedness. (*Note added 1925.*)

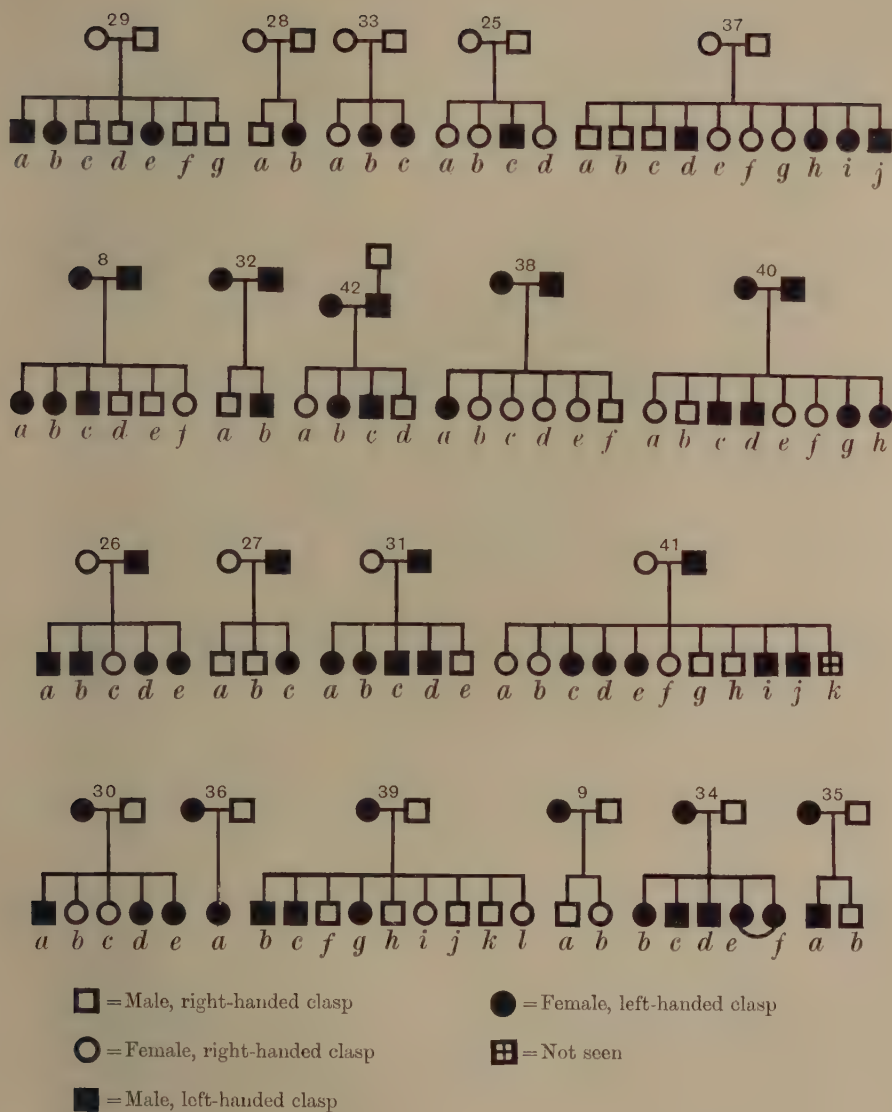


Fig. 128. Hand-clasp in the Burbage Families.

and 49 lefts. In fact, there seems to be an equality of rights and lefts all round, no matter what the parents are. Neither does there seem to be any question of sex limitation or linkage, for out of the 67 males and 73 females concerned there are 37 right males, 34 right females, 30 left males, and 39 left females. Naturally the question arises whether in a case of this kind we are really dealing with an hereditary character at all, and yet it is difficult to imagine that a perfectly discontinuous, congenital, and apparently instinctive character like hand-clasp is not inherited.

One thing, however, seems clear, and that is, that the inheritance, if any, is not Mendelian, at any rate so far as one can analyse it from the data. Somatic segregation is evident, but there is no dominance, and above all, no gametic purity, so far as one can see. It is often pointed out, with truth, that dominance is not an essential part of Mendelism, only segregation matters. The case of hand-clasp, however, suggests that even segregation (somatic) is not always evidence of Mendelian heredity, but that pure breeding alone is the true test. The case of hand-clasp is particularly interesting inasmuch as it is, so far as the writer knows, the only human character investigated that defies Mendelian analysis, and as such it appears to constitute a single real exception to the general rule.

A comparison of figs. 127 and 128 shows at a glance that in dealing with the inheritance of right and left-handedness, and right and left hand-clasp, we are up against two totally different characters, and that, however much they may appear to resemble one another superficially, their fundamental natures must be wide asunder.

Tuberculosis.

In venturing to touch upon such an intricate and complicated question as tuberculosis, the writer is well aware of the many difficulties involved, but the question is of such overwhelming importance that a few observations noted while conducting other researches in the same families may possibly be of some interest to those engaged in a study of the question from the point of view of Eugenics.

The pedigrees (fig. 129) of the adult Burbage families that have suffered from the disease deal only with pulmonary tuberculosis and comprise three definite categories:—

First, those who have died from the disease.

Second, those who are seriously affected with it.

Third, those who have resisted it.

The first and second categories are alas self-evident. The third category consists of adult individuals who, so far, have proved themselves resistant to infection, in the sense that the disease, if present at all, has never seriously affected them, though it has proved fatal in their homes.

From the point of view of heredity, the significance, if any, of the above facts seems to lie in the following observations:—

First, when both parents are resistant to the disease (*i.e.*, have come under infection but have not been seriously affected by it) and yet have one or more children who have succumbed to its ravages, the death-rate is about one-fourth. Thus out of 78 adult children of such parents, 18 died of the disease, 3 have been seriously affected by it, and 57 have so far proved resistant.

Second, the single case in which both parents died of the disease produced 7 children, of whom 4 have died of the disease, 2 have been seriously affected by it, and 1 has so far proved resistant.

Is it possible that the power of resistance to tuberculosis in certain individuals is due to the presence of a definite factor which is absent in those who succumb to the disease? Owing to the extraordinary difficulties which beset this question the above suggestion is only submitted with a note of interrogation, in the hope that some expert student of tuberculosis will apply it and test it in a more extended form, with due regard to the many environmental complications involved.

Musical Temperament.

That certain individuals have a natural disposition for music, while others have not, is evident to the most casual observer. That this natural disposition or temperament is innate and hereditary there can be little doubt. Musical associations and careful training can, of course, do much in enriching the musical qualities in an individual of a musical disposition, but in the absence of the musical temperament these outer stimuli are practically powerless. My observations in the Burbage families go to show that individuals with a natural disposition for music almost always display it early in life, usually between the 2nd and 6th year. Musical children soon pick up airs and melodies after hearing them a few times and are found constantly humming them over to themselves, almost unconsciously. So far as my experience goes, non-musical children do not do this, when they are not silent they either drone monotonously or are merely noisy. Musical children as they grow up begin to harmonise naturally, putting in their own

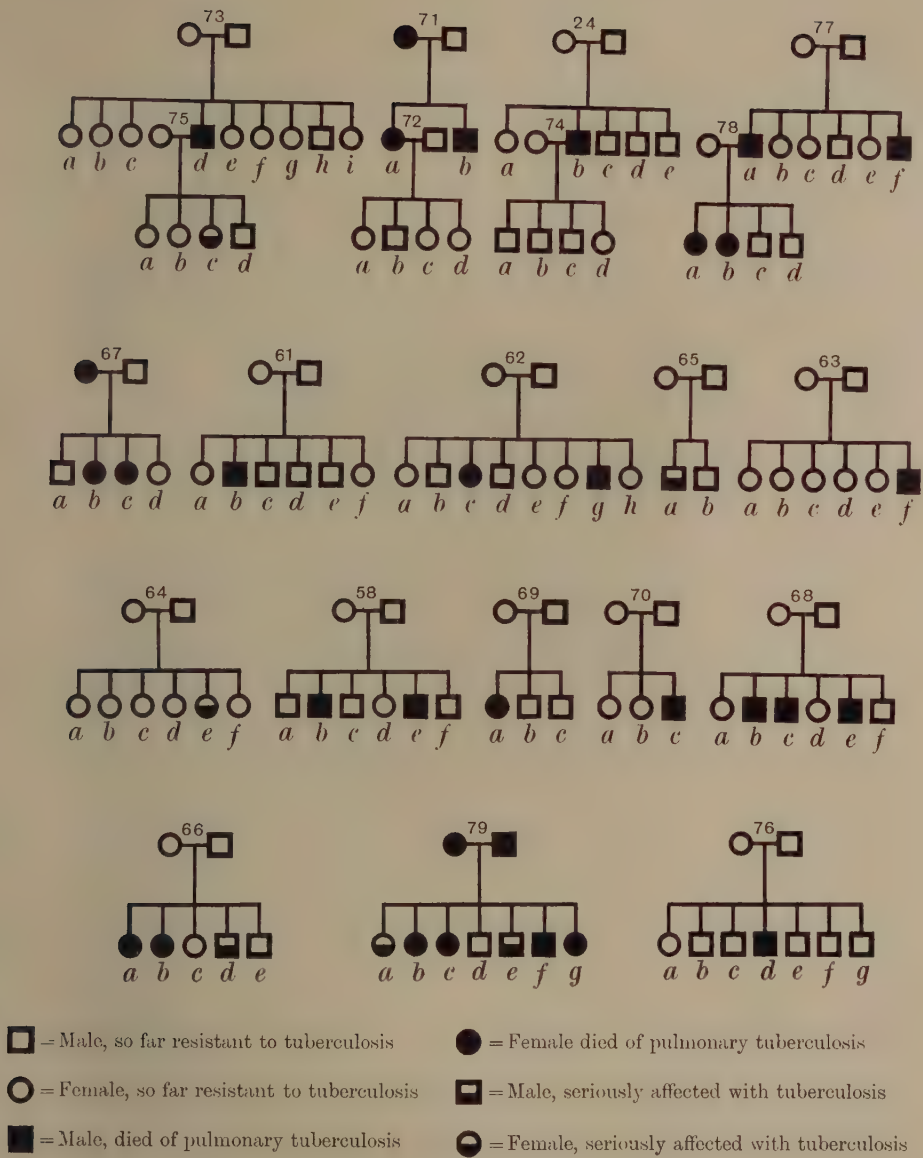


Fig. 129. Tuberculosis in the Burbage Families.

parts without any tuition. If their singing voice is poor they may take up the playing of some instrument, otherwise they are content with mere humming or whistling.

In musical children and adults all this is done naturally and spontaneously without conscious effort and in many cases without knowing a note of music throughout their lives. Of course, in all musical individuals there are found varying degrees of ability in regard to powers of expression, musical memory, sense of time and rhythm and other musical *minutiae*, all of which may be developed to a considerable extent by careful training. There appears also to be a distinct class of non-musical individuals who are practically tone-deaf, who for instance are unable to distinguish between the "National Anthem" and the "Old Hundredth," and to whom apparently there is little, if any, distinction between low and high notes. Such cases, however, are rare, probably as rare as the talented musician among ordinary musical people. There seems also to be a striking difference between musical and non-musical persons in the nature of their ordinary speaking voice, the musical individual speaks naturally in melodious tones, the voice rising and falling with correct intervals, while the non-musical individual speaks naturally in monotones without a trace of melody. So far, only one case has been observed by the writer where a non-musical individual has a melodious speaking voice, and not a single case where a musical individual has a monotonous voice.

A study of the distribution of musical and non-musical individuals in the Burbage families led the writer (15) to point out in 1908 that the musical temperament appeared to behave as a Mendelian recessive character, the ordinary non-musical temperament being dominant. For it was found that when both parents were musical all the children were musical. When neither parent was musical *either* none of the children was musical, *or* a few were musical and most of them were not. When one parent was musical and the other not, *either* none of the children was musical, *or* about one-half were musical and one-half not (see p. 290).

Professor F. O. Grover, of Oberlin College, U.S.A., has kindly informed me that his investigations in American families confirm the above results. Further observations made here since 1908 generally confirm and extend the previous work. One interesting case, however, has recently turned up which seems to be an exception to the rule that when both parents are musical all the children are musical. This is the case of a boy in family 35*b* (fig. 130), 7 years old, who though fond of singing, cannot at present sing an air at all correctly. Whether

this is due to some defect of control of the vocal chords, or whether it is due to a non-musical temperament is a question that may be decided at a later stage. This boy's elder brother is a sweet and correct singer with an undoubted musical temperament, as are both his parents.

The pedigrees in fig. 130 will serve to illustrate the genetics of the musical and non-musical temperaments.

All the individuals classed as "musical" in the pedigrees have given some definite expression of their musical temperament, in one way or another, either as singers, players, whistlers or hummers. On the other hand, the individuals classed as "non-musical" have not done so, that is, so far as my observation of them has gone. It is, of course, possible that a few of those classed as "non-musical" may be of the nature of mute musicians (especially those early affected with deafness), but in any case, if such do exist they must be rare. The pedigrees given serve to illustrate the dominance of the non-musical and the recessive nature of the musical temperament, the segregation of these two characters in the same family and the apparent purity of the extracted recessives.

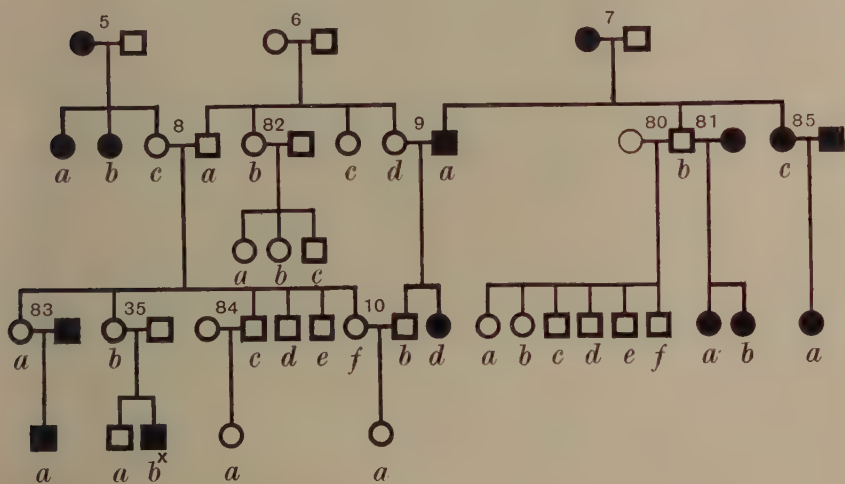
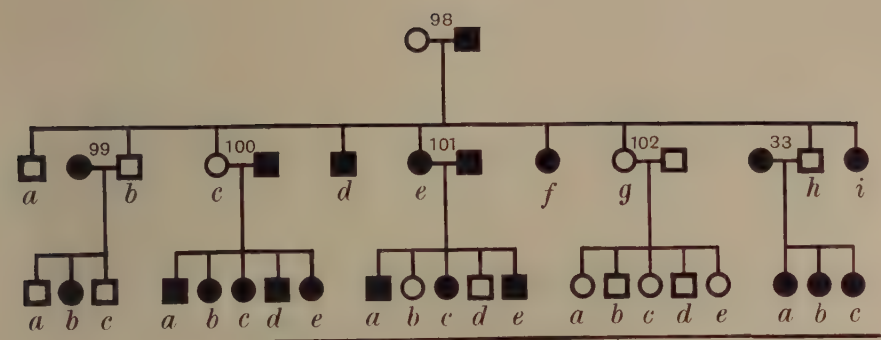
The above results raise two interesting points:—

First, the fact that the musical temperament is inherited on Mendelian lines is interesting because as a temperamental character it is probably of a different order from purely physical or structural characters like pigmentation and left-handedness and the question naturally arises if a psychological character like musical temperament follows simple Mendelian rules, may not other characters of a similar nature, but more important perhaps to the race from the Eugenic standpoint, do so also? This opens up possibilities of a wider field of research for the worker in human Genetics and Eugenics.

Second, the fact that the musical temperament behaves as a recessive character and not a dominant, would seem to imply, according to the "presence and absence" method, that an individual is non-musical owing to the presence of an inhibitory factor preventing the expression of the musical temperament which is hypostatically present in everyone.

In other words, it would appear that while probably everyone possesses the fundamental musical temperament, yet owing to the presence of an inhibitory factor non-musical people are unable to give expression to it, whereas, on the other hand, in the absence of such an inhibitor the musical temperament is expressed and the individual is musical.

The interesting question as to whether an individual with a double



□ = Male, with musical temperament

■ = Male, non-musical

○ = Female, with musical temperament

● = Female, non-musical

Fig. 130. Musical Temperament in the Burbage Families.

dose of the inhibitory factor differs in any way from an individual with a single dose, cannot be answered on the present evidence. It is tempting, however, to suppose that a tone-deaf person differs in gametic constitution from an ordinary non-musical individual.

Genetics and Eugenics.

In the above paper on Mendelian heredity in Man, an attempt has been made to show how the new principles of Genetics can be applied to Man with some degree of success. In studying the inheritance of the more simple physical characters in Man, it is evident that we are as yet only feeling our way towards the solution of certain larger and more complicated problems which are of vital importance to the human race. The future of Eugenics depends very largely on the solution of these problems. I do not wish for one moment to suggest that the art of Eugenics has been born before its time, but I do feel that before we can venture to apply the scientific principles of Genetics to human life we must first make our foundations sure. For this reason, I am convinced that a good deal of spade work in human Genetics will have to be done before any considerable amount of practical good can be accomplished in Eugenics. Eugenics is simply applied Genetics, and *sound Eugenics can only be founded on sound Genetics.*

NOTE ADDED 1925.

ON THE SEX-DISTRIBUTION OF MENDELIAN EYE-COLOURS IN A
LOCAL AREA IN MIDLAND ENGLAND.

In first demonstrating the Mendelian Inheritance of Eye-colour in Man at the British Association in August 1907 (see p. 284) and in my subsequent papers (see pp. 272, 286, 391) only data of genetical value at that time were published.

My observations and studies of eye-colour in the Burbage district of Leicestershire and Warwickshire were not confined to these inasmuch as they included families with one child, childless parents, natural children, orphans in the schools and so on, none of which could be usefully included in genetical data.

It has recently been suggested to me that it might be useful from the anthropological and statistical points of view to publish a full record of my observations in this local area, and, in view of the suggestion that eye-colour in Man may be partially sex-linked in its inheritance, I have taken the opportunity to give also the sex-distribution of the Duplex and Simplex types of eye-colours observed.

General Distribution in the Area.

Out of a population of about 3000 the number of individuals examined was 1569, which were taken at random¹.

Of these 961 had eyes with duplex pigmentation and 608 had eyes with simplex pigmentation.

812 were males (including 1 probable intersex) and 757 were females.

There were 476 Duplex males, 485 Duplex females, 336 Simplex males and 272 Simplex females.

Parents and Offspring.

Out of the 1569 individuals examined 1341 belonged to the 215 families of parents and their offspring which were observed and studied for genetical results.

Of these 813 had Duplex eyes and 528 had Simplex eyes.

689 were males and 652 were females.

There were 392 Duplex males, 421 Duplex females, 297 Simplex males and 231 Simplex females.

Miscellaneous Individuals.

The remaining 228 individuals examined could not be used for genetical studies for various reasons as they included childless parents, orphan children, widows and widowers with and without children and so on.

Of these 148 had Duplex eyes and 80 had Simplex eyes. 123 were males and 105 were females.

There were 84 Duplex males, 64 Duplex females, 39 Simplex males and 41 Simplex females.

Parents of the Genetical Families.

In the 215 Genetical Families studied, of the 430 individual parents 258 had Duplex eyes and 172 had Simplex eyes.

115 were Duplex males, 143 were Duplex females, 100 were Simplex males and 72 were Simplex females.

Offspring of the Genetical Families.

The 215 Genetical Families studied produced 911 offspring.

Of these 555 had Duplex eyes and 356 had Simplex eyes.

474 were males and 437 were females.

¹ In no case was there a preferential selection of Duplex or Simplex families, but for the genetical data the largest families of faithful matrons were selected, and preference was given to native families with three or four living generations and their collateral descendants, so that on the whole the large sample of the population examined may be said fairly to represent a "random selection" of the families of the district.

There were 277 Duplex males, 278 Duplex females, 197 Simplex males and 159 Simplex females.

Matings of the Parents of the Genetical Families.

Of the 215 matings of the Parents of the Genetical Families,

78 were Duplex females with Duplex males,

35 were Simplex females with Simplex males,

65 were Duplex females with Simplex males and

37 were Simplex females with Duplex males.

Offspring of Duplex ♀ × Duplex ♂ (78 families).

Of the 347 offspring of Duplex parents 316 were Duplex and 31 were Simplex.

171 were males and 176 were females.

There were 155 Duplex males, 161 Duplex females, 16 Simplex males and 15 Simplex females.

Of the 78 families with Duplex parents, 22 families gave 106 Duplex and Simplex offspring.

Of these 75 were Duplex and 31 were Simplex.

50 were males and 56 were females.

There were 34 Duplex males, 41 Duplex females, 16 Simplex males and 15 Simplex females.

The remaining 56 families of these matings gave 241 Duplex offspring of which 121 were males and 120 were females.

Offspring of Simplex ♀ × Simplex ♂ (35 families).

Of the 147 offspring of Simplex parents, all were Simplex.

82 were males and 65 were females.

Offspring of Duplex ♀ × Simplex ♂ (65 families).

Of the 252 offspring of Duplex mothers and Simplex fathers,

158 were Duplex and 94 were Simplex,

133 were males and 119 were females.

There were 82 Duplex males, 76 Duplex females, 51 Simplex males and 43 Simplex females.

Of the 65 families with Duplex mothers and Simplex fathers, 41 families gave 181 Duplex and Simplex offspring and of these 87 were Duplex and 94 were Simplex.

96 were males and 85 were females.

There were 45 Duplex males, 42 Duplex females, 51 Simplex males and 43 Simplex females.

The remaining 24 families of these matings gave 71 Duplex offspring of which 37 were males and 34 were females.

Offspring of Simplex ♀ × Duplex ♂ (37 families).

Of the 165 offspring of Simplex mothers and Duplex fathers,

81 were Duplex and 84 were Simplex.

88 were males and 77 were females.

There were 40 Duplex males, 41 Duplex females, 48 Simplex males and 36 Simplex females.

Of the 37 families with Simplex mothers and Duplex fathers,

34 families gave 155 Duplex and Simplex offspring.

Of these 71 were Duplex and 84 were Simplex.

84 were males and 71 were females.

There were 36 Duplex males, 35 Duplex females, 48 Simplex males and 36 Simplex females.

The remaining 3 families of these matings gave 10 Duplex offspring of which 4 were males and 6 were females.

An analysis of these 3 families shows that the Duplex father in one case is certainly heterozygous for Simplex, while in another case only 1 child was produced, so that the Duplex father may have been heterozygous in this case also.

This leaves a solitary but substantial family of 8 children in which the Duplex father is apparently homozygous while all the remaining Duplex fathers mated with Simplex mothers (36) are (with one possible exception) heterozygous for Simplex. On the other hand there seems to be a due proportion of both homozygous and heterozygous Duplex females. If it were established that all Duplex males are heterozygous for Simplex it might be supposed that the dominant factor *D* for Duplex pigmentation of the iris is sex-linked in Man, were it not for the fact (as shown above) that the eye-colours of all matings on the whole are normally distributed among the sexes and do not seem to follow at all the *Drosophila* scheme of *XY* sex-linked inheritance (see footnote p. 347).

The comparative scarcity of the matings of Duplex fathers with Simplex mothers, as compared with the matings of Duplex mothers and Simplex fathers, is no doubt due to the general excess of Simplex males over Simplex females which is marked throughout the genetical data and calls for further investigation.

REFERENCES.

1. Bateson, W. *Mendel's Principles of Heredity* (Camb. Univ. Press), 1909, ch. vi. pp. 107—110; ch. xii. pp. 205—234.
2. Darbishire, A. D. *Breeding and the Mendelian Discovery* (Cassell & Co.), 1911, ch. iv. pp. 40—49.
3. Davenport, G. C. and C. B. "Heredity of Eye-Colour in Man," *Science*, 1907 (Nov. 1st), Vol. 26, pp. 589—592.
4. „ "Heredity of Hair-form in Man," *Amer. Nat.*, 1908 (May), XLII. pp. 341—349.
5. „ "Heredity of Hair-Colour in Man," *Amer. Nat.*, 1909 (April), XLIII. pp. 193—211.
6. „ "Heredity of Skin Pigment in Man," *Amer. Nat.*, 1910 (Nov. and Dec.), XLIV. pp. 641—672, 705—731.
7. „ *Eugenics* (Holt & Co., New York).
8. Doncaster, L. *Heredity in the Light of Recent Research* (Camb. Univ. Press), 1910, ch. viii. pp. 99—115.
9. Drinkwater, H. "An Account of a Brachydactylous Family," 1908, *Proc. Roy. Soc. Edin.*, xxviii. p. 35.
10. Farabee, W. C. "Inheritance of Digital Malformations in Man," *Papers Peabody Museum Amer. Arch. and Ethn. Harv. Univ.*, 1905, III. p. 69.
11. Goddard, H. H. "Heredity of Feeble-mindedness," 1910, *Amer. Breed. Mag.*, I. pp. 165—178.
Amer. Breed. Assoc., 1910, pp. 103—116 (reprint).
Eugenics Review, 1911, III. pp. 46—60 (reprint).
12. Gossage, A. M. "The Inheritance of Certain Human Abnormalities," *Quart. Journ. Med.*, 1908, p. 331.
13. Hurst, C. C. A Reference to the Mendelian Nature of Eye-Colour in Man, *Nature*, 1907 (Sept. 26th), Vol. 76, p. 558.
14. „ "On the Inheritance of Eye-colour in Man," 1908, *Proc. Roy. Soc., B.* Vol. 80, pp. 85—96.
15. „ "Mendel's Law of Heredity and its Application to Man," 1908, *Trans. Leic. Lit. and Phil. Soc.*, XII. Pt. 1, pp. 35—48.
16. Jordan, H. E. "Inheritance of Left-Handedness," 1911, *Amer. Breed. Mag.*, II. pp. 19—29.
17. „ "A Comparative Microscopic Study of the Melanin Content of Pigmented Skins," 1911, *Amer. Nat.* (Aug.), XLV. pp. 449—470.
18. Lutz, F. E. "The Inheritance of the Manner of Claspings the Hands," *Amer. Nat.*, 1908 (March), XLII. pp. 195—6.
19. Mudge, G. P. "On Segregation in the Second Generation of Crosses between Red and White Races of Man," *Nature*, 1907, Nov. 7th, p. 9.
20. „ "Segregation of European Skin Colour," *Mendel Journal*, 1909, No. 1, p. 24.
21. Nettieship, E. "Hereditary Diseases of the Eye" (Bowman Lecture), *Trans. Ophthalm. Soc.*, 1909, XXIX. pp. lvii—cxviii.
22. Punnett, R. C. *Mendelism* (Macmillan), 1911 (3rd ed.), ch. xii. pp. 120—122; ch. xv. pp. 156—170.
23. Salaman, R. N. "Heredity and the Jew," *Journ. Genetics*, 1911, I. pp. 273—292; *Eugenics Rev.*, 1911, III. pp. 187—200.

XXX

MENDELIAN EXPERIMENTS WITH THOROUGHBRED HORSES¹

Amid all the conflicting opinions on light-horse breeding there appear to be two definite points on which most authorities are agreed.

First: that the best sort of light-horse for purposes of general utility is the Hunter.

Second: that the best foundation stock from which to breed the Hunter is the British Thoroughbred.

The usual method employed is to mate "half-bred" mares with Thoroughbred stallions. Experience shows, however, that the Hunter cannot be bred with any degree of certainty on these lines. To the Mendelian such a failure is only to be expected, because the "half-bred" mares, on account of their mixed breeding, are likely to be heterozygous and may, consequently, throw a large proportion of "misfits." Mendelism has taught us that to get uniform results in breeding the parents must be homozygous, i.e., *with like germ-cells*, and not heterozygous, i.e., *with unlike germ cells*. "Pure-breds" are naturally more likely to be homozygous than "half-breds." In order, therefore, to breed Hunters true, the most likely way to succeed will be to breed solely from the Thoroughbred.

It is a common error, however, to suppose that any, or all, Thoroughbreds will do for the purpose of breeding Hunters. On the contrary, my own observations show that while some Thoroughbreds constantly throw excellent Hunters, others throw but a few, and some none at all. To the Mendelian these facts are significant, for they imply that, as regards Hunter qualities some Thoroughbreds are homozygous while others are heterozygous.

Of the various kinds of offspring thrown by Thoroughbred sires and dams, the nearest approach to the Hunter, so far as performance goes, is the 'Chaser that runs under National Hunt Rules in England and Ireland. These 'Chasers have demonstrated their ability to carry a good weight safely over a mixed country at a racing pace, which, after

¹ Communicated to the *Bloodstock Breeders' Review*, I. pp. 86—90 (1912), at the request of Lieut.-Col. Dealtry Part and the Editor.

all, is the primary qualification required in a Hunter. Following Mendelian methods, if individual Thoroughbreds can be found that constantly throw 'Chasers, the first step toward the making of a breed of homozygous Thoroughbred Hunters will be accomplished.

It will be noted that in Mendelian methods of breeding everything turns on the germinal or gametic constitution of the animals bred from. To the Mendelian it is not what a horse looks like, nor what it has done, nor how it is bred even, that determines its breeding value, *but simply and solely what kind of offspring it throws*. In this respect Mendelian methods differ fundamentally from ordinary practice. Once homozygous true-breeding animals are found they can be mated together and a homozygous line established which may be relied upon to breed true without any further selection.

In this case, the particular problem is to segregate from the mass of homozygous and heterozygous Thoroughbreds, homozygous individuals of both sexes that will constantly throw 'Chasers. A study of the parents and relatives of weight-carrying winners of long distance 'chases under National Hunt Rules during the last few years has revealed the existence of such material, though, as might be expected, the numbers are few and apparently confined to certain strains. One strain is particularly noteworthy, inasmuch as three generations in the direct maternal line have produced 26 'Chasers out of 27 runners. The only runner of this line not a 'Chaser is the 4-year old hurdler, "Ballyhist" not yet put to 'chasing¹. It is remarkable that no fewer than 13 of these 'Chasers are by "Hackler." Table I gives a summary of the racing record of the 26 'Chasers of the "Mount Royal" line.

Another strain presents two generations in the direct maternal line producing to various sires, 9 'Chasers out of 10 runners. The only runner of this line not a 'Chaser is "Lady Bree," who ran in one hurdle race, and it may be noted that the 'Chaser "Diadem" only ran in one 'chase.

Table II gives a summary of the racing record of the 9 'Chasers of the "Mavourneen" line.

Two individual mares, "Faithful Lassie" and "Athela," have been found which give 5 runners each, all of which were 'Chasers. One of these "Strawberry Queen," only ran in one 'chase. Table III gives a summary of the racing record of the 10 'Chasers from these two mares.

¹ "Ballyhist" was put to 'chasing in 1913 and won 7 steeplechases from 1913—1915. (Note added 1924.)

TABLE I.

First Generation.

Produce of MOUNT ROYAL (Monarch of the Glen—Keerawn).

	Chases run	Won	Value £	Maximum distance mi. fur.	Maximum weight carried st. lb.	Placed 2nd & 3rd	Failed to finish
Citadel (by Ingomar)	9	4	664	3 4	12 6	3	1
Cyclops (by Concha)	12	6	363	3 0	12 0	3	0
Cinnamon (by Concha)	9	1 ¹	245 ²	2 0	10 13	6	0
Senlac (by Atheling)	26	9	543	3 0	12 5	6	3
Williamstown (by Atheling)	7	0	—	—	—	1	1

Second Generation.

Produce of CIRCE (Play Actor—Mount Royal).

Innisfallen II ³ (by Ireland)	2	0	—	3 0	—	0	1
Young Buck (by Buckingham)	18	2	200	3 0 ⁴	12 0	4	4
Flaxman (by Hackler)	12	4	155	3 4 ⁶	11 4	4	0
Springbok (by Springtime)	38	8 ⁵	1336	3 0	12 6	10	5
Old Fairy House (by Hackler)	16	6	833	3 0	12 0	4	2
Cackler (by Hackler)	15	11	2717	3 0	12 7	4	0
Flaxseed (by Hackler)	6	3	188	2 0	11 12	2	1
Distaff ⁷ (by Hackler)	5	0	—	—	—	3	1

¹ Dead-heat.² Stakes divided.³ To Stud.⁴ Fourth in Grand National.⁵ Fifth in Grand National.⁶ Four years old.⁷ One win disqualified.

TABLE I (continued).
Produce of CINNAMON (Concha—Mount Royal).

	Chases run	Won	Value £	Maximum distance mi. fur.	Maximum weight carried st. lb.	Placed 2nd & 3rd	Failed to finish
Brown Hackle ¹ (by Hackler)	8	2	45	2 ³ 4	10 7	2	0
Covert Hack (by Hackler)	34	8	1407	4 0 ³	13 5	8	2
Ballyhack (by Ireland)	3	2	85	3 0	10 3	0	1
Cee Spring (by Springtime)	4	1	21	2 1	10 7	1	0
Killester (by Hackler)	14	1	49	2 4	12 9	4	4
Carder (by Hackler)	14	0	—	—	—	3	1
Cinna (by Laveno)	11	0	—	—	—	3	3
Covert Coat* (by Hackler)	10	1	417	4 0	11 0	3	1

Third Generation.

Produce of BALLYMACARNEY (Royal Meath—Cinnamon).

Doggie (by Hackler)	27	11	587	3 0	12 2	9	2
Ballyhackle (by Hackler)	44	11	884	3 2	13 0	21	6
Ballymacoll (by Hackler)	24	7	390	2 0	12 10	14	2
Ballymadun (by Bushey Park)	10	1	397	3 0	11 0	4	1
Ballymacad* (by Laveno)	8	4	271	2 0	12 8	1	2

¹ Sent to Germany at 4 years old.

² 5 years old.

³ Seventh in Grand National.

* Since the above Tables were compiled in 1912 many more steeplechases have been won by many of these horses. As representatives of the "Mount Royal—Cinnamon—Ballymacarney" line it is peculiarly fitting that "Covert Coat" and "Ballymacad" should have completely confounded the "racing" critics of the above scheme (see *Bloodstock Breeders' Review*, 1912, pp. 28–30, 90–92) by winning the "Grand National" in 1913 and the "War National" in 1917. "Covert Coat" also completed the "Grand National" Course in 1914 and "Ballymacad" run 3rd in 1918 in spite of being struck into and lamed during the race. With such a promising start it is indeed unfortunate that owing to War conditions and the absence of Lt.-Col. Dealtry Part and the author on military service from 1914 to 1919, the experiments came to an untimely end. (Note added 1924.)

TABLE II.

First Generation.

Produce of MAVOURNEEN (Master Richard—Amulet).

	'Chases run	Won	Value £	Maximum distance mi. fur.	Maximum weight carried st. lb.	Placed 2nd & 3rd	Failed to finish
Coronet (by Blood Royal) ...	15	11	2943	3 0 ¹	13 12	2	1
Diadem (by Ingomar) ...	1	0	—	—	—	0	0
Ireland (by Rostrevor) ...	13	8	2112	4 0	13 7	3	0
Innisfail (by Rostrevor) ...	11	2	664	4 0	12 1	7	1
² Breemount's Pride (by Kendal) ...	22	5	2183	3 4 ²	10 12	4	3
Pride of Bree (by Enthusiast) ...	30	7	427	3 0	12 13	10	2
Breemount (by St Gris) ...	16	1	98	3 4	12 4	8	1

Second Generation.

Produce of BREEMOUNT'S PRIDE (Kendal—Mavourneen).

Hackmount (by Hackler) ...	22	14	548	3 0	12 8	6	1
Judina (by Hackler) ...	23	4	221	3 0	11 12	8	5

¹ Sixth in Grand National.² Fourth in Grand National (fig. 131).

TABLE III.

Produce of FAITHFUL LASSIE (Ascetic—Faith).

	Chases run	Won	Value £	Maximum distance mi. fur.	Maximum weight carried st. lb.	Placed 2nd & 3rd	Failed to finish
Faithless Lad (by Derncleugh)	45	11	843	3 0	12 5	15	6
Fidessa (by Hackler)	26	4 ¹	268 ²	3 0	11 13	14	1
Shanawan (by Bushey Park)	23	6	405	3 0	12 6	7	4
Besom (by Bushey Park)	14	4	305	2 0	12 1	5	2
Hazle Twig (by Bushey Park)	2	1	53	2 0	10 9	1	0

¹ Two dead-heats.² Stakes divided.

Produce of ATHELA (Atheling—Aileen Ogue).

Strawberry Queen (by Little John)	1	0	—	—	—	0	0
Lord Chatham (by Little John)	30	5	886	3 4	12 3	9	3
Frigate (by Red Prince II)	36	16	836	3 0	13 3	11	1
Turco III (by Red Prince II)	4	1	54	3 0	10 10	1	1
Rosy Cross (by Ray's Cross)	3	0	—	—	—	1	0

The fact that these 8 Thoroughbred mares, put to 18 different sires, have given at least 45 'Chasers out of 47 runners, and not a single "flat-racer," is rather remarkable in view of the mixture of "flat-racers," hurdlers, and 'Chasers usually thrown by Thoroughbred mares to Thoroughbred sires. It may possibly be urged that none of these 47 runners had the opportunity of showing what they could do on the flat; but in face of the economic fact that a "flat-racer" can win so much more money than a 'Chaser, and at an earlier age too, it is hardly conceivable that the astute trainers who handled these 47 runners, would allow such a golden opportunity to slip through their fingers, and it seems reasonable to presume that these 47 runners were more suitable for 'chasing.

In any case however, the main point is, that the race-course test proved that practically all the offspring of these 8 mares were 'Chasers. From the Mendelian standpoint such a result is of considerable significance. First of all it shows that in these particular strains at all events, the inborn aptitude which goes to make a 'Chaser when properly trained, is represented in the germ-cells either by a single factor, or by a complex of factors which behave as a unit in heredity.

At present we have no knowledge whatever of the nature of the Mendelian unit that goes to make a 'Chaser, nor do we know precisely how a 'Chaser differs germinally from a "flat racer." All we know is that a hereditary unit is concerned in the matter, and, further, that it must exist in a homozygous condition either in the dam, or the sire, or both, in each mating. We do not yet know whether this 'Chaser unit is due to the presence of an epistatic factor, i.e. *a dominant character*, or to its absence, i.e. *a recessive character*. This can only be determined by breeding experiments on Mendelian lines with some of these 'Chasers and their offspring.

The Mendelian problem to be solved, therefore, is whether these homozygous horses are homozygous dominants or homozygous recessives. Thanks to the keen interest and kind generosity of Captain Dealtry C. Part, of the 21st Lancers, it has been possible to put these Mendelian experiments into operation this season. Mr F. W. Carter, Superintending Inspector of the Board of Agriculture, who has been detailed by the Board to watch and assist the experiments on their behalf, has also rendered valuable aid.

The following animals have so far been purchased:—

(1) The mare "Ballymacarney" to represent the "Mount Royal" line; she has now a chestnut colt foal by "St Gris," and has been put to "Perigord."



Fig. 131. Brood Mare "Breemount's Pride,"

By "Kendal" out of "Mavourneen."

Winner of five steeplechases value £2183 and fourth in the Grand National Steeplechase.

Dam of two winning 'chasers and of foal below.

(Photographed at Burbage.)



Fig. 132. Bay Colt Foal,

By "Creangate" out of "Breemount's Pride" (fig. 131).

(Photographed at Burbage.)

(2) The mare "Breemount's Pride" (fig. 131) to represent the "Mavourneen" line, together with her yearling colt by "Missel Thrush," and her "Hackler" daughter's yearling colt and two-year-old filly by "Creangate." "Breemount's Pride" has now a bay colt foal by "Creangate" (fig. 132), and has been put to "St Aidan."

(3) The mare "Frigate" to represent "Athela" and "Red Prince II" is still in training.

Another mare may be purchased later to represent "Faithful Lassie" and "Bushey Park" or "Hackler." The mare, "Revolving Light," by "Red Prince II" out of "Revolver" by "Hawkeye," was independently bought by Captain Part, and though not strictly included in the experiments, will be kept under observation, and has been put to "Perigord."

In these Mendelian experiments it will, of course, be necessary to test the germinal nature of the above animals and their offspring by mating them with heterozygous as well as homozygous sires. All the progeny raised will be tested, so far as possible, on the race-course under both rules.

Owing to the common practice of cutting colts put to 'chasing, it has not been possible to obtain a homozygous male of any of the above lines for use this season. This raises an important practical question, for if all 'Chaser colts are to be cut, it means that our future supply of weight-carrying thoroughbreds will be considerably curtailed. Many owners and trainers seem to regard this unfortunate practice as necessary. That it is a great convenience in some respects there can be no doubt, but in view of the fact that the Grand National has been won at least fourteen times by an entire horse, and that during recent years entire horses have completed the Aintree course at least nineteen times, the absolute necessity for cutting 'Chaser colts is not so apparent. Indeed, it would be easy to produce statistics to show that entire horses have, comparatively, made a better show than geldings over the Grand National course.

If Captain Part's experiments succeed in establishing a homozygous line of Thoroughbred 'Chasers, the primary qualities required in a Hunter will be fixed. The next step will be to breed from these a homozygous line of Thoroughbred Hunters, by eliminating certain secondary characteristics possibly present in the 'Chaser, but undesirable in the Hunter, such as, for instance, unsoundness, bad conformation, and ill manners, while still retaining at all costs, the primary qualities in a homozygous state.

In my opinion too much importance should not be attached to uniformity of type. Practical experience of hunting in Leicestershire has long ago convinced me that true Hunter qualities have less to do with physical conformation than is generally supposed. Good Hunters are of all shapes and sizes, and many good weight-carriers are comparatively light in bone. The handsome show Hunter with its perfect conformation may give one a comfortable ride, but it does not follow that it will be able to hold its own in a fast run across a big country.

It is the mental and moral qualities of a Hunter or 'Chaser, rather than the purely physical properties that tell in the long run. A perfect physical conformation is useless without the "jumping temperament," and its concomitant mental state, and the possession of moral courage in a trial of endurance is often a greater asset than a powerful physique.

In conclusion, an interesting side issue, arising out of Captain Part's Mendelian experiments, may be mentioned. It seems probable that in the process of determining the germinal nature of the homozygous 'Chaser, the results obtained in the course of the experiments may indirectly lead us to a knowledge of the germinal constitution of "flat-racers" generally. It is not impossible that such knowledge may provide a key to the solution of the problem of breeding a Classic Winner.



Fig. 133. The National Sweet Pea Society's Trials at Burbage, 1912.
Collection of 254 Seed Stocks germinated in small pots.

"ROGUES" IN SWEET PEAS¹

Since the introduction of the beautiful "Spencer" forms of Sweet Peas the practical difficulty of securing true stocks, permanently free from "rogues," has caused much concern to the raisers, growers, and distributors of Sweet Pea seeds and to Sweet Pea fanciers generally.

When inspecting the National Trials at Sutton Green in 1911, I was much impressed by the large number of colour "rogues" present in many of the stocks. The most puzzling feature, however, to a mere Mendelian, was the presence of such large numbers of *dominant* colour "rogues." One naturally expected to find recessive colour "rogues" in the heterozygous or "unfixed" stocks, but one was hardly prepared to see so many dominant colour "rogues" among the carefully selected stocks sent by the leading raisers.

The question, therefore, seemed to be worth investigation, both from the Mendelian standpoint and the economic point of view, and to this end experiments were initiated at Burbage. In order to investigate the nature of the various "rogues" appearing in the "Spencer" Sweet Peas, three different classes of material have been used:—

(1) SUPERIOR COMMERCIAL STOCKS OFFERED IN 1911—12.

These consisted of a representative collection of 206 stocks of 150 varieties grown from seed sent out by the leading growers and distributors. For the most part these were purchased in the raiser's original packets, but several firms very kindly presented me with packets of their novelties for trial. This material provides an illustration of the general purity of the superior stocks sent out in 1911—12.

(2) THE NATIONAL TRIALS CARRIED OUT AT THE BURBAGE EXPERIMENT STATION IN 1912.

These consisted of a representative collection of 254 stocks, made up for the most part of certain novelties and superior forms submitted by raisers to the judgment of the experts on the Floral Committee of the National Sweet Pea Society in 1912. This material provides an illustration of the general purity of the newer stocks, the best of which will eventually supersede existing varieties (fig. 133).

¹ Read at the Fourth Conference of the National Sweet Pea Society, London, Oct. 13th, 1912, and reprinted from *The Sweet Pea Annual*, 1913.

(3) MENDELIAN STOCKS GROWN AT THE BURBAGE EXPERIMENT
STATION IN 1912.

These consisted of 43 "pure-line" stocks of 13 leading varieties in 12 distinct colours. Each "pure-line" stock was saved from a single homozygous plant, but the flowers were not covered up at all, nor were the plants isolated from one another, or from other colours, except in so far that certain groups of colours were grown on separate plots.

Those containing blue sap, for instance, were grown at a distance of 100 yards from the others, and the Whites and Creams were planted together at one end of the plot of red sap colours, while the yellow sap colours were planted at the other end.

This material provides an illustration of the general purity of stocks grown by the more refined methods of "pure-line" breeding, though, owing to the flowers being uncovered, it provides no true test of gametic constitution.

The following Tables I, II, and III give the general results in 1912. The colour classification is that adopted by the Floral Committee of the National Sweet Pea Society for 1913. The Tables show in each Colour section:—(1) Number of varieties grown (except in Table II); (2) number of stocks; (3) number of plants; (4) number of True plants observed; (5) number of "Rogue" plants; (6) number of Type "Rogues"; (7) number of Colour "Rogues"; (8) number of Dominant Colour "Rogues"; (9) number of Recessive Colour "Rogues."

A comparison of the totals of the three tables shows a marked difference in the proportion of "rogues" in the three classes of material. For while the Commercial Stocks gave about 108 per thousand, and the National Trials 114 per thousand, the Mendelian Stocks gave less than 6 per thousand.

The chief cause of this marked difference is to be found in the total absence of type "rogues" and recessive colour "rogues" in the Mendelian Stocks. On the other hand, in the Commercial Stocks there were about 69 type "rogues" and 34 recessive colour "rogues" per thousand, while in the National Trials there were about 61 type "rogues" and 40 recessive colour "rogues" per thousand.

It may be useful at this point to define what is meant by a "type rogue."

TABLE I. "Rogues" in Commercial Stocks, 1912.

Colours	Varieties	Stocks	Plants	True	Rogues	Type Rogues	Colour Rogues	Dominant Colour Rogues	Recessive Colour Rogues
Bicolor	...	1	31	31	14	6	9	3	6
Blue	10	186	172	5	1	4	1	3
Blush	...	6	89	84	1	1	1	1	1
Carmine	...	3	60	59	16	14	4	4	—
Cerise	...	3	95	79	41	32	9	9	—
Cream, Buff and Ivory	...	13	212	171	5	1	5	4	1
Cream-Pink (pale)	...	8	131	129	44	—	44	—	44
Cream-Pink (deep)	...	13	247	203	1	1	1	1	1
Crimson	...	7	130	129	1	1	2	1	1
Fancy	...	3	114	112	2	29	9	—	9
Lavender	...	6	218	185	33	—	4	—	4
Lilac...	...	4	66	62	4	5	8	4	4
Magenta	...	7	112	101	11	—	4	1	3
Marbled and Watered	...	11	111	107	4	—	1	—	1
Maroon	...	9	133	132	1	—	6	—	6
Maroon (Purple)	...	3	50	44	6	4	1	—	1
Maroon (Red)	...	3	46	24	22	21	1	—	1
Mauve (dark)	...	3	79	73	6	6	5	—	5
Mauve (pale)	...	6	107	102	5	4	6	6	—
Orange Pink	...	9	143	121	22	18	—	—	—
Orange Scarlet	...	5	108	108	—	—	1	—	1
Picotee Edged (Cream ground)	...	4	47	46	1	—	7	—	7
Picotee Edged (White ground)	...	8	101	93	8	1	35	1	34
Pink (deep)	...	9	236	201	35	1	—	—	—
Pink (pale)	...	2	43	43	—	—	—	—	—
Rose...	...	2	64	64	—	—	—	—	—
Salmon Shades	...	16	371	323	48	42	43	43	—
Scarlet	...	14	281	274	7	6	4	4	—
Striped and Flaked (Purple and Blue)	...	1	60	60	—	—	5	1	1
Striped and Flaked (Chocolate on Grey)	...	2	34	29	5	—	1	—	—
Striped and Flaked (Red and Rose)	...	1	21	20	1	—	1	—	1
White	...	12	210	130	80	80	—	—	—
		206	3939	3511	428	272	219	82	137
Per Thousand	891.3	108.6	69.0	55.5	20.8	34.7

TABLE II. "Rogues" in the National Trials at Barbage, 1912.

Colours	Stocks	Plants	True	Rogues	Type Rogues	Colour Rogues	Dominant Colour Rogues	Recessive Colour Rogues
Bicolor	6	116	110	6	—	6	—	6
Blue ...	18	378	329	49	24	31	8	23
Blush	2	41	32	9	—	9	3	6
Carmine	4	79	58	21	15	7	2	5
Cerise	17	338	307	31	19	22	7	15
Cream, Buff and Ivory	6	123	117	6	3	3	3	—
Cream-Pink (pale) ...	19	382	361	21	3	21	9	12
Cream-Pink (deep)	10	193	184	9	—	9	3	6
Crimson	8	158	155	3	3	—	—	—
Fancy	3	65	60	5	—	5	—	5
Lavender	10	188	124	64	48	26	2	24
Lilac ...	6	111	103	8	2	8	7	1
Magenta	6	126	121	5	2	5	1	4
Marbled and Watered	14	269	193	76	53	24	8	16
Maroon	5	104	92	12	—	12	—	12
Maroon (Purple)	3	62	54	8	—	8	—	8
Maroon (Red)	6	127	110	17	—	2	2	—
Mauve (dark)	11	214	190	24	1	24	5	19
Mauve (pale)	12	239	167	72	55	37	15	22
Orange-Pink	15	298	286	12	4	9	8	1
Orange-Scarlet	5	123	123	—	—	—	—	—
Picotee Edged (Cream ground)	3	62	59	3	—	3	3	—
Picotee Edged (White ground)	1	23	23	—	—	—	—	—
Pink (deep) ...	7	139	127	12	—	12	—	12
Pink (pale) ...	9	175	170	5	2	5	5	—
Rose ...	4	83	82	1	—	1	1	—
Salmon Shades	14	277	252	25	19	6	3	3
Scarlet	6	125	125	—	—	—	—	—
Striped and Flaked (Purple and Blue)	8	161	131	30	21	10	9	1
Striped and Flaked (Chocolate on Grey)	2	44	44	—	—	—	—	—
Striped and Flaked (Red and Rose)	4	87	80	7	1	7	2	5
White	10	196	154	42	41	2	—	2
	254	5106	4523	583	316	314	106	208
Per Thousand	885.8	114.1	61.8	61.4	20.7	40.7

TABLE III. "*Rogues*" in *Mendelian Stocks* at *Burbage*, 1912.

Colours	Varieties	Stocks	Plants	True	Rogues	Type Rogues	Colour Rogues	Dominant Colour Rogues	Recessive Colour Rogues
Blue	1	65	65	—	—	—	—	—
Blush	4	1261	1261	—	—	—	—	—
Cream	2	605	605	—	—	—	—	—
Cream-Pink (pale)	...	1	182	182	—	—	—	—	—
Crimson	4	1366	1366	—	—	—	—	—
Maroon	5	1164	1164	—	—	—	—	—
Orange-Pink	2	496	496	—	—	—	—	—
Orange-Scarlet	...	9	1316	1316	53	—	53	53	—
Pink (deep)	2	380	380	—	—	—	—	—
Pink (pale)	8	969	969	—	—	—	—	—
Salmon Shades	...	1	168	168	—	—	—	—	—
Scarlet...	...	4	815	815	—	—	—	—	—
	15	43	8840	8787	53	—	53	53	—
Per Thousand	9940	59	—	59	59	—

TABLE IV. "*Rogues*" in Table III.

(Orange-Scarlet Stocks.)

Variety	Stocks	Plants	True	Rogues	Colours
Thomas Stevenson ...	51 A	184	184	—	—
" " ...	51 B	167	167	—	—
" " ...	51 D	150	150	—	—
" " ...	51 E	97	95	2	1 Deep Pink & 1 Orange-Pink
" " ...	51 G	162	162	—	—
" " ...	51 H	55	54	1	Deep Pink
" " ...	51 I	120	118	2	Deep Pink
Edna Unwin ...	60 A	148	148	—	—
" " ...	98 A	286	238	48	Dark Mauve
	9	1369	1316	53	

TYPE ROGUES.

To the modern Sweet Pea fancier, a "type rogue" is a plant bearing flowers which are not of the true "Spencer" type. The true "Spencer" type has large flowers (except in some Salmon and Scarlet shades), with the standard and wings waved or frilled, and an open keel. The open keel is the hall-mark of the true "Spencer." In the old—so-called "grandiflora"—type, the keel is closed, the stamens and pistil being closely clamped together at the apex. In the modern "Spencer" type the keel is loose and open at the apex, causing the pollen to shed within the keel and the pistil to protrude. (This distinct difference of structure may possibly account for the large amount of sterility manifested by the "Spencer" varieties in a wet season like that of 1912, for I observed that while most of the type rogues with clamped keels set seed pods freely at Burbage in 1912, there was not an ounce of seed of the "Spencer" varieties on three acres of ground! On the other hand, in the dry season of 1911 the "Spencer" varieties were sufficiently fertile for single plants to produce from 400 to 500 seeds each, while the same season some of the single plants of the clamped keel type produced from 800 to 1000 seeds each.)

It will be understood, therefore, that the term "type rogue" in the above tables refers to those plants which bear flowers with a clamped

keel, the "true" plants being of the "Spencer" type bearing flowers with an open keel. The type rogues observed are, of course, variable in other respects; a few have hooded standards, while in others the standards are erect, others again have slightly waved standards, while in most the standards are quite plain. All, however, resemble one another in having clamped keels.

From experiments carried out at Burbage, it is evident that the clamped keel behaves as a single Mendelian character dominant (epistatic) to the open keel of the "Spencer" type, which is recessive (hypostatic). Consequently if seed be carefully saved from plants with open keels only, and all clamped keels are eliminated from the seed-grounds, no "type rogues" should appear at all in our Sweet Pea cultures. In view, however, of the known behaviour of certain recessive cream and white Sweet Peas which *when crossed* may give rise to dominant Red and Purple colours, the possibility of a dominant "type rogue" arising from an outside cross between two recessive Spencers must not be overlooked, but so far there is no evidence of the occurrence of such a thing, and the possibility seems rather remote judging from my own results, in which 43 plants of the Spencer type growing together, uncovered, did not give a single "type rogue" in 8840 plants, though some cross-fertilisation undoubtedly took place, as will be seen later.

From a practical point of view I think we may safely say that there is no reason why a "type rogue" with a clamped keel should appear in either Commercial seed stocks or in the National Trials. From the definite manner in which the "type rogues" appear, in large numbers in certain stocks of Commercial seed and in the Trials and hardly at all in others, it is evident that care has not been taken to eliminate these rogues from the seed-grounds.

The practical advantage of realising that the "type rogue" is a Mendelian dominant is, that no matter how mixed in type a certain stock may be, if the dominants are rogued out properly the stock will breed perfectly true to the recessive Spencer type. There will consequently be no need to discard such a stock because it is mixed in type, nor will there be any need to attempt to "refix" it from single plants. The whole stock can be safely utilised for seed provided that the dominant "type rogues" are all eliminated from the crop as soon as they appear.

A reference to Tables I and II shows, that out of a total number of 1011 rogues in the Commercial Stocks and in the National Trials, no

less than 588 are "type rogues." The elimination of the "type rogues" from our Sweet Pea cultures would, therefore, get rid of at least one-half of the rogues now existing.

COLOUR ROGUES.

"Colour rogues" may be conveniently divided into two classes, Dominant (epistatic) and Recessive (hypostatic). Dominant "colour rogues" are those whose colour characters are known to be dominant to the colour characters of the parent stock; that is to say, their colour is due to the presence of a higher factor or factors added to those present in the parent stock. Recessive "colour rogues" are those whose colour characters are known to be recessive to the colour characters of the parent stock; that is to say, their colour is due to the absence of a higher factor or factors present in the parent stock.

The Mendelian experiments with various colours of Sweet Peas carried out at Cambridge and at Burbage, during the last ten years, have provided a useful and ready means of classifying the "colour rogues" of Sweet Peas into Dominants and Recessives. For instance, cream is the lowest recessive colour known, white is dominant to cream, tinged white to white, pink to tinged white, crimson to pink, and maroon to crimson, while the wild purple bicolor is dominant to all colours. Orange and salmon shades are dominant to white and cream, but recessive to pink and crimson. All the purple and blue shades are dominant to the red shades from which the blue factor is absent. Purple maroon is dominant to maroon, maroon to mauve and lavender, and lavender to deep and pale blue.

With regard to the colour patterns; bicolors, with light-coloured wings, are dominant to selfs, with dark-coloured wings; while picotees, marblings, stripes and flakes are apparently recessive to selfs and bicolors.

In investigating the origin of "colour rogues" in Sweet Peas their classification into Dominants and Recessives has been particularly helpful, for it is evident that a dominant rogue may arise from a different cause from that which produces a recessive rogue.

DOMINANT COLOUR ROGUES.

In Table I, out of 219 "colour rogues," 82 are dominants, and of these no less than 43 are in the salmon section. Further analysis shows that 35 of these are rosy-salmon rogues in "Stirling Stent," all of which are "type rogues" with clamped keels. In the early stage these rogues might be easily passed over, especially if the keels were not examined,

and there can be little doubt that the presence of these 35 dominant "colour rogues" is due to faulty roguing in the seed grounds. The origin of the remaining "colour rogues" in Table I is not so clear. Possibly a few may be due to accidental mixture in harvesting and distribution, yet, in view of the care usually bestowed by expert growers and distributors, accidents of this kind must be so rare in the material used as to be almost negligible.

Next to the Salmon section in Table I the Cream section shows the largest number of dominant "colour rogues." Some of these are maroon, mauve, and rose bicolors, all with red axils, in a stock of "Clara Curtis." These rogues are of peculiar interest, for we can safely say that their presence is not due either to accidental mixture or to faulty roguing, because these purple and red rogues in the cream stock were observed to come from *seeds with light-coloured skins*, proving that they were gathered from either a cream or a white mother plant. The fair presumption is that they were gathered from "Clara Curtis" plants. If they had been gathered from purple or red rogues, or were accidental mixtures, they would certainly have come from dark-coloured seeds.

A precisely similar case is found in Table II, in No. 17 of the National Trials, where an unnamed cream stock produced dominant red rogues with red axils, from seeds with light-coloured skins.

Now from the Cambridge experiments we know that red colour in Sweet Peas is due to the simultaneous presence of two complementary colour factors known as *C* and *R*, while purple colour is due to the addition of a third factor, *B*. On the other hand, a cream Sweet Pea lacks either *C* or *R* or both, while *B* may be present or absent. From this it follows that a self-fertilised cream plant can only give creams, and that the only way a purple or red rogue can be produced from a cream plant is by the introduction of a second colour factor, by cross-fertilisation, either with another cream or white plant, or with a purple or red-coloured plant.

Therefore it is evident that all the dominant purple and red rogues coming from light-coloured seeds in the cream stocks are due to cross-fertilisation.

There can, I think, be little doubt that most of the other dominant "colour rogues" in Tables I, II, and III are due to the same cause. At all events, no other explanation seems possible in the case of the 53 dominant "colour rogues" in the Mendelian stocks in Table III. All the seeds of these stocks were carefully saved from single plants grown

3 ft. by 4 ft. apart, thus eliminating entirely the possibility of the presence of odd rogues among the stock plants. Nor was there any chance of accidental mixture with these stocks, for the pods from each plant were carefully picked and shelled into a small, lidded cardboard box in which the seeds remained until they were sown. Further, all the stock plants were bred from homozygous stocks, and themselves behaved as such, throwing no recessive rogues in 8840 plants.

Therefore it would appear that the presence of these 53 dominant rogues was due to the accidental cross-fertilisation of odd flowers on the mother plants in 1911, by some means unknown.

This conclusion can, of course, be fully tested by the Mendelian method of selfing some of these dominant rogues. If the above conclusion is correct, these dominant rogues will, when selfed, throw orange-scarlet recessives. A number of these rogues were isolated and the whole plants covered up with muslin cages; unfortunately, owing to the unfavourable season, not a seed formed in the cages, and only a few odd pods in the open. Several thousand cuttings, however, were put in during the autumn, of the dominant rogues and "pure-line" stocks, in the hope of getting seed from them next year, in order to continue the experiments.

In view of this explanation, it may be of interest to examine these dominant colour rogues further. Table IV gives the actual numbers of the rogues thrown by each plant and their colours. It will be observed that these rogues only appear in one colour section out of the twelve, *i.e.*, the Orange-scarlet section, and in both the varieties grown, *i.e.*, "Thomas Stevenson" and "Edna Unwin." Again, out of nine "pure-line" stocks concerned, only four threw rogues, and these rogues were of three colours, orange-pink, deep pink, and dark mauve. The respective proportions were: orange-pink, 1 in 97; deep pink, 1 in 97, 1 in 55, and 2 in 120; dark mauve, 48 in 286.

Curiously enough no rogues at all appeared in the Orange-scarlet section in either the Commercial stocks (Table I), or the National Trials at Burbage (Table II) this year, though I understand that a single dominant "colour rogue" appeared at Sutton Green in this colour section, while last year (1911) I observed that in the Trials, dominant "colour rogues" were numerous and varied in the original stock of "Thomas Stevenson" which had previously proved to be perfectly true, and, indeed, was so at Burbage last year.

The proportions in which the dominant rogues appeared in the Mendelian stocks varied from about 1 in 6 to 1 in 97, and give no

indication of a Mendelian ratio. These details all go to confirm the idea that these dominant "colour rogues" were due to accidental cross-fertilisation. How the foreign pollen was conveyed from one plant to another is quite unknown. No doubt some kind of insect was concerned in the matter. The suspected Leaf-cutter Bee (*Megachile*) was observed among the mother plants in 1911 in small numbers, but no Hive Bees were noticed. *Bombi*, however, were fairly numerous, and the small beetle (*Meligethes*), and Earwigs also, were frequently found in the flowers, but information is wanting as to the possibilities of these insects carrying pollen from one plant to another, except perhaps in the case of the Leaf-cutter Bee.

In this connection it may be interesting to record the positions occupied by the mother plants that threw the dominant rogues, and their minimum distances from plants of other colours likely to produce these particular rogues by cross-fertilisation. The plant 51E was only 4 feet distant from the nearest orange-pink plant, while 51E, 51H, and 51I were each 12 feet distant from the nearest deep pink plant. On the other hand, 98A was no less than 104 yards distant from the nearest plant known to be carrying the blue factor. It may be noted that 98A was the last plant of the last row of a plot, and was the most accessible plant to an insect visitor coming from the plot where the blue saps were growing. In this case it would appear that the pollen was conveyed by a mobile insect of considerable flying powers and to a single plant only, while in the other cases the distance to be traversed was short, and several adjacent plants were contaminated, so that possibly ground insects might be the culprits.

RECESSIVE COLOUR ROGUES.

Recessive "colour rogues" will, naturally, be expected in a heterozygous or "unfixed" stock, and a careful examination of the three tables shows that many of the recessive rogues appearing in the Commercial stocks and in the National Trials, are clearly of this nature. In Table I, for instance, it will be observed that in the deep cream-pink and the deep pink sections no less than 78 recessive "colour rogues" appear, representing more than one-half of the total number of recessive "colour rogues" in the Commercial stocks. The majority of these 78 recessive "colour rogues" can be traced to those well known heterozygous varieties "Miriam Beaver," "Syeira Lee," and "Audrey Crier." Experiments at Burbage show that these varieties are permanently heterozygous and quite unfixable, the deep cream-pink shade being the

F₁ hybrid between a pale cream-pink and an orange-pink, much in the same way that a Blue Andalusian fowl is an F₁ hybrid between a black and a splashed white.

The Blue Andalusian fowl and the "Miriam Beaver" Sweet Pea, being Mendelian hybrids, can never breed true, but will always throw the light and dark forms, on the average one-quarter of each. The light and dark colours will, of course, each breed true, and the middle or hybrid form can always be obtained by crossing the light and dark colours together.

In the case of the "Miriam Beaver" Sweet Pea, however, this would hardly be worth while from an economic point of view, as so much time and trouble would be involved in remaking the variety each year.

The remaining recessive "colour rogues" in Table I, and also in Table II, are no doubt mostly due to the presence of ordinary heterozygous "unfixed" stocks that can be "fixed" by the selection of homozygous plants in the ordinary Mendelian way. Table III illustrates this point clearly, as not a single recessive rogue appears in 8840 plants, owing to the homozygous nature of the mother plants.

Apart from the question of "unfixed" stocks, however, recessive "colour rogues" might also arise from accidental mixture, or from accidental cross-fertilisation, as in the case of the dominant "colour rogues." We have already shown that while the former cause is almost negligible, the latter cause is undoubtedly one that has to be seriously considered. If dominant "colour rogues" arise in this way, then recessive "colour rogues" may also be expected to arise in the same way, but with this important difference, that while the dominant rogues will certainly appear in the first year after accidental cross-fertilisation, the recessive rogues will not appear until the second year after cross-fertilisation.

It is to be expected, therefore, that a few of the Mendelian stocks in Table III will throw some recessive rogues in 1913. The importance of this point will be realised by the following calculation. Presuming that an equal number of dominants and recessives were caused by accidental cross-fertilisation in 1911, then, as 53 dominant rogues appeared in 1912, there would also be 53 heterozygous or impure plants carrying recessive "colour rogues," but these rogues would not be perceived in 1912 owing to their recessive nature. In 1913, each of these 53 contaminated plants would throw on the average 25 per cent. of recessive rogues, so that if each plant produced 100 seeds, no less than 1325 recessive rogues would be expected to appear in these stocks in 1913.

There is no doubt that this possibility of accidental cross-fertilisation goes far to explain many mysteries in Sweet Pea growing. One can see now quite clearly how it is that a careful grower who has apparently a perfectly true stock of a certain variety one year, finds that in the following year it contains a number of rogues, and all through no fault of his own.

PRACTICAL APPLICATION.

The practical question now arises as to how far a knowledge of these results can be applied by the grower in his attempts to keep his stocks true and free from rogues. A comparison of Table III with Tables I and II suggests that the adoption of Mendelian "pure-line" methods of breeding would, at all events, reduce the numbers of rogues from about 100 per thousand to about 5 per thousand; 100 rogues per thousand means, on the average, 1 rogue in every packet of 10 seeds, while 5 rogues per thousand only means 1 rogue in every 20 packets of seed.

Further, if the seed cultures could be made biologically clean, by covering up the flowers from accidental cross-fertilisation, there is no doubt that rogues would not appear at all, and the stocks would breed absolutely true. I fear, however, that this would not be an economic proposition, as the cost would prove prohibitive, and for the sake of five rogues per thousand it would hardly be worth while.

As a practical summary, the following suggestions are made for the benefit of the grower of Sweet Peas for seed. To carry out these will no doubt entail a little more trouble, time and care, but the results obtained thereby should more than compensate for the extra work.

- (1) Save all *stock* seed from single plants, grown not less than 3 ft. apart each way.
- (2) For *stock* seed use only plants from a homozygous (true breeding) stock.
- (3) When growing bulk seed, let the stock seed from each single plant be sown separately, but side by side. This will give an opportunity of dealing separately with those stocks in which the rogues may appear.
- (4) For both stock and bulk seed, let each colour be grown at least 100 yards distant from any other.
- (5) Allow no "type rogues," with clamped keels, to be on or near the seed grounds.

XXXII

THE APPLICATION OF GENETICS TO ORCHID BREEDING¹

The new science of Genetics has been built up during the past decade on the firm foundations laid by Mendel nearly fifty years ago. The Royal Horticultural Society, through its far-seeing Secretary, the Rev. W. Wilks, took a leading part in the introduction of Mendel's work to English readers some twelve years ago, and in the meantime the Society has in many ways helped to advance the new science of Genetics.

It is therefore fitting that the Orchid Conference held to-day under the auspices of the Society should have the opportunity of discussing the question of the application of Genetics to Orchid breeding.

The word "Genetics" was first used by Professor Bateson at the time of the International Hybridisation Conference held by the Royal Horticultural Society in London in 1906, and was used by him as a convenient word to express the modern science of breeding on Mendelian lines. Technically the word "Genetics" covers not only the primary principles of heredity as understood and expounded by Mendel himself, but also the secondary developments of Mendelism that have taken place during the past decade in consequence of the experiments and observations of Mendelians in all parts of the world not only with cultivated plants, but also with domesticated animals, including Man himself.

Perhaps the most remarkable feature in the progress of the modern science of Genetics is the extraordinary way in which experiments with plants have led to the solution of important problems in animal breeding; while, on the other hand, experiments with animals have in their turn led to the solution of many difficulties in plant breeding. As experiment follows experiment, and discovery succeeds discovery, the word "Genetics" will still cover the ground, and its influence and utility will become increasingly marked as time rolls on.

¹ Read at the Second Orchid Conference, London, Nov. 6th, 1912, and reprinted from *Orch. Conf. Rep., Journ. Roy. Hort. Soc.* xxxviii. pp. 412—429 (1913).

Orchids are truly regarded as the aristocrats of the plant world, and the results achieved by Orchid breeders during the past twenty years constitute one of the seven wonders of the world of horticulture. No other family of cultivated plants has yielded so many beautiful hybrids in so short a time as the Orchidaceæ. A reference to the "*Orchid Stud-Book*"¹ shows that at least 40 genera and 300 distinct species have been already utilised by Orchid breeders in the making of their hybrids. About 2000 of these are primary hybrids, while no fewer than 300 are generic hybrids. Besides these botanical hybrids, there are on record some thousands of horticultural—secondary and multiple—hybrids, to say nothing of multitudinous varietal and individual forms which no man can number.

When one remembers that most of these remarkable results have been achieved in less than a generation (one might almost say, since the last Orchid Conference was held), and that the raising of such delicate exotics from seed under purely artificial conditions is by no means an easy matter even for the expert, one cannot but admire the practical genius of British and Continental Orchid breeders that has brought about such a consummation. Those who had the good fortune to see the remarkable display of Orchids at the International Exhibition at Chelsea last May must have been impressed by the leading part played by hand-raised hybrids in the various groups.

In face of such an imposing array of beautiful hybrids it may seem presumptuous on the part of a student of Genetics to offer to the Orchid breeder any suggestions as to the advantages that might be derived from an application of the science of Genetics to Orchid breeding, for where practical Orchid breeding has been so successful the application of the science of Genetics might naturally be regarded as somewhat superfluous. But those behind the scenes know better. The wonderful hybrids that appear in public represent only one side of the picture.

Orchid breeders of experience know too well that in order to secure a really first-class hybrid it is necessary to raise large numbers of others. Many are raised, but few are chosen. Some crosses naturally yield more good forms than others, but generally speaking first-class hybrids are few and far between, and the moderate and poor forms are far too numerous. In secondary and more complex hybrids especially, the number of misfits and unwanted weeds that turn up time after time is rather disconcerting, and the question often arises as to whether many

¹ *The Orchid Stud-Book* by R. A. Rolfe and C. C. Hurst, 1909, 327 pp. with 120 figs.

of these crosses are worth making at all from the economic point of view, though from the scientific standpoint they are naturally most instructive.

OLD AND NEW METHODS.

From this it is evident that chance plays a great part in modern Orchid breeding, and there is really very little certainty in the game as played by the leading exponents. Now, if the modern science of Genetics teaches anything, it is that there are *certainities* to be found in breeding. A careful study of recent work in Genetics points unmistakably to the important fact that law and order may be perceived in breeding. From the economic point of view it costs just as much to raise a poor form as it does a good one, the time, trouble, and expense involved are the same, and the practical problem that faces the Orchid breeder is how to manage his matings so as to reduce the number of worthless forms to a minimum.

This is where the application of Genetics to Orchid breeding should come in to help the breeder. Of course, in the early stages of the application it cannot be expected that all Orchid breeding will be reduced to a certainty, that would be too much to expect; nor would it be altogether desirable, for in such a case Orchid breeding would be divested of much of its charm. Already a few certainties in Orchid breeding are known, thanks mainly to the application of the Mendelian principles, and that many other certainties await discovery there can be no doubt.

One important point, however, should be noted, and that is that under present conditions Orchid breeders must very largely discover these certainties for themselves by the application of the principles of Genetics. In this respect Orchid breeding differs much from ordinary plant breeding. The Orchid field is so wide, the conditions so difficult, and the complications so numerous, that only a practical expert can carry out the necessary experiments, and even he must have considerable resources of capital and experience at his command.

In order to apply Genetics to Orchid breeding it will be necessary for the Orchid breeder to make himself familiar with the first principles. These principles are now universally accepted by all serious students of heredity who have experimented for themselves, and they can be applied equally to all kinds of plants and animals, including Man himself. From the practical point of view it will not be necessary for the Orchid breeder, at the outset at all events, to venture much

beyond these first principles. His own experiments, if based on these principles and carefully carried out, will soon yield a harvest of valuable data that will lead him on to more advanced work and to a deeper insight into the possibilities and certainties of Orchid breeding.

FIRST PRINCIPLES OF GENETICS.

Each plant or animal is composed of many characters, most of which are heritable.

Each heritable character is represented in the germ-cells by one or more factors.

In the fertilised cell (*zygote*) each factor is present either in a double state or a single state.

When a double dose of the factor is present, the plant or animal is called *homozygous*, or pure in regard to that factor.

When a single dose of the factor is present, the plant or animal is called *heterozygous*, or impure in regard to that factor.

When the factor is altogether absent, the plant or animal may be called *zerozygous*, or wanting in regard to that factor.

Previous to fertilisation, the germ-cells divide, and *segregation* takes place in regard to each factor.

Each cell with a *double* dose of the factor becomes two fertilising-cells (*gametes*), each with a *single* dose of the factor.

Each cell with a *single* dose of the factor becomes two fertilising-cells (*gametes*), one of which has a *single* dose of the factor and the other has *none*.

Fertilisation consists in the union of two fertilising-cells (*gametes*), a pollen or sperm cell from the male uniting with an egg-cell from the female.

If both paternal and maternal gametes have a *single* dose of the factor, a zygote will be formed with a *double* dose of the factor, and the plant or animal will be *homozygous*, or pure in regard to that factor.

If, however, one of the gametes has a *single* dose of the factor and the other has *none*, a zygote will be formed with a *single* dose of the factor, and the plant or animal will be *heterozygous*, or impure in regard to that factor.

If *neither* of the gametes has the factor at all, it will of course be altogether absent from the zygote, and the plant will be *zerozygous*, or wanting in regard to that factor.

PRACTICAL CONSEQUENCES.

The practical consequences of these first principles of Genetics are that, as regards any one heritable character represented by a factor, there are three distinct kinds of individual plants: (1) homozygous, or pure; (2) heterozygous, or impure; and (3) zerozygous, or wanting. Each of these three kinds of individuals will give a different result when bred from. With regard to outward appearance, (3) will as a rule be easily distinguishable from (1) and (2), representing as it usually does the hypostatic or recessive form, from which the epistatic or dominant character is quite absent.

If, as sometimes happens, a single dose of the dominant factor produces the same effect in the zygote as a double dose, we get the phenomenon of complete dominance, and in such cases (1) and (2) are indistinguishable in outward appearance, and their pure or impure nature can only be determined by breeding from them.

If, however, as often happens in Orchids, a single dose of the dominant factor produces a different effect in the zygote from a double dose, we get the phenomenon of incomplete dominance. In such cases (1) and (2) are distinguishable in outward appearance, and their pure or impure matter is determined at sight without breeding from them.

The apparent blending of characters observed in many Orchid hybrids is no doubt due to the effect of the single dose of one factor reacting on the effect of a single dose of another factor, resulting in a mosaic.

When more than one heritable character is involved in the breeding problem, as usually happens in Orchids, the different kinds of individual plants become exceedingly numerous. One plant, for instance, may be pure for one character, impure for another, and wanting for a third character, and so on. Each individual plant, however, has a definite germinal constitution, which can be ascertained by cross-breeding it with other plants. In this way a factorial analysis of the two plants can be made, and, as regards each heritable character, each plant will be found to be either pure (homozygous), impure (heterozygous), or wanting (zerozygous), and as such it will behave when bred from. Once the factorial analysis of a plant has been made, all future breeding from that plant is reduced practically to a certainty.



Fig. 134. *Cattleya Gaskelliana* Rchb. f. ex Williams var. *Alba* Williams (cc R.R. Albino).

(*Orchid World*.)

COLOUR AND ALBINISM.

Recent results show that in certain cases an apparently simple heritable character is due to the presence of more than one distinct factor. For instance, in Orchids we have already one case of that description, and no doubt there are many more yet undiscovered. From evidence collected by the author during the past five years¹, there can be little doubt that the rosy-purple colour present in the flowers and leaves of the various species of *Cattleya* and *Cypripedium* is due to the simultaneous presence of two complementary colour factors, which we call C and R. If one or both of these factors is absent, the result is a true albino, with no trace of purple sap in the flowers and leaves. This purple colour can only be produced when the two factors C and R are both present.

Now, as we have just seen, the colour factors C and R may be present in a double state—CC and RR—or in a single state—Cc and Rr—or they may be absent altogether—cc and rr; consequently no less than five different kinds of albinos may exist, as follows:

- (1) CCrr,
- (2) Cerr,
- (3) ccRR (fig. 134),
- (4) ccRr,
- (5) cerr.

For the sake of convenience it is usual in Genetics to represent the presence of a factor by a capital letter and its absence by a small one.

These five albinos may be absolutely identical in appearance and outward characters, yet each has a different germinal constitution, and consequently will give different results in breeding. Each of these five albinos will breed true to albinism when selfed, but when they are crossed *inter se*, different results will be obtained. Thus, out of the fifteen possible matings, eleven will give all albinos, two will give on the average equal numbers of albinos and coloured forms, one will give one coloured form to three albinos, and one will give all coloured forms.

Table I gives the factorial details of these fifteen matings, showing how the above calculations have been made.

C represents first colour factor.

R represents second colour factor.

¹ Bateson, W., *Mendel's Principles of Heredity* (1909), pp. 96—97. (See *supra*, pp. 294—299.)

CC and RR represent double presence of factors C and R—*i.e.*, homozygous, or pure.

Cc and Rr represent single presence of factors C and R—*i.e.*, heterozygous, or impure.

cc and rr represent absence of factors C and R—*i.e.*, zerozygous, or wanting.

TABLE I. *Albino Matings.*

Parents	Offspring	Result
(1) CCrr × (1) CCrr	All CCrr	All Albinos
(1) CCrr × (2) Ccrr	1 CCrr : 1 Ccrr	All Albinos
(1) CCrr × (3) ccRR	All CcRr	All Coloured
(1) CCrr × (4) ccRr	1 CcRr : 1 Ccrr	1 Coloured : 1 Albino
(1) CCrr × (5) cccr	All Ccrr	All Albinos
(2) Ccrr × (2) Ccrr	1 CCrr : 2 Ccrr : 1 cccr	All Albinos
(2) Ccrr × (3) ccRR	1 CcRr : 1 ccRr	1 Coloured : 1 Albino
(2) Ccrr × (4) ccRr	1 CcRr : 1 ccRr : 1 Ccrr : 1 cccr	1 Coloured : 3 Albinos
(2) Ccrr × (5) cccr	1 Ccrr : 1 cccr	All Albinos
(3) ccRR × (3) ccRR	All ccRR	All Albinos
(3) ccRR × (4) ccRr	1 ccRR : 1 ccRr	All Albinos
(3) ccRR × (5) cccr	All ccRr	All Albinos
(4) ccRr × (4) ccRr	1 ccRR : 2 ccRr : 1 cccr	All Albinos
(4) ccRr × (5) cccr	1 ccRr : 1 cccr	All Albinos
(5) cccr × (5) cccr	All cccr	All Albinos

The same scheme of course applies equally to coloured forms as to albinos. Thus four distinct kinds of coloured forms are possible, viz.:

- (a) CCCR,
- (b) CCRr,
- (c) CcRR,
- (d) CcRr.

These four coloured forms may be absolutely identical in appearance and outward characters, yet each has a different germinal constitution, and consequently will give different results in breeding. Of the ten possible matings, five will give *all* coloured forms, four will give on the average three coloured forms to one albino, and one will give on the average nine coloured forms to seven albinos.

Table II gives the factorial details of these matings, showing how the above calculations have been made.

Further interesting results will be obtained by mating the four coloured forms with the five albino forms.

Of the twenty possible matings, seven will give *all* coloured forms, eight will give on the average equal numbers of coloured and albino

forms, two will give three coloured forms to five albinos, two will give three coloured forms to one albino, and one will give one coloured form to three albinos.

TABLE II. *Coloured Matings.*

Parents	Offspring	Result
(a) CCRR × (a) CCRR	All CCRR	All Coloured
(a) CCRR × (b) CCRR	1 CCRR : 1 CCRr	All Coloured
(a) CCRR × (c) CcRR	1 CCRR : 1 CcRR	All Coloured
(a) CCRR × (d) CcRr	1 CCRR : 1 CCRr : 1 CcRR : 1 CcRr	All Coloured
(b) CCRr × (b) CCRr	1 CCRR : 2 CCRr : 1 CCrr	3 Coloured : 1 Albino
(b) CCRr × (c) CcRR	1 CCRR : 1 CCRr : 1 CcRR : 1 CcRr	All Coloured
(b) CCRr × (d) CcRr	1 CCRR : 1 CcRR : 2 CCRr : 2 CcRr : 1 CCrr : 1 Ccrr	6 Coloured : 2 Albinos
(c) CcRR × (c) CcRR	1 CCRR : 2 CcRR : 1 ccRR	3 Coloured : 1 Albino
(c) CcRR × (d) CcRr	1 CCRR : 1 CCRr : 2 CcRR : 2 CcRr : 1 ccRR : 1 ccRr	6 Coloured : 2 Albinos
(d) CcRr × (d) CcRr	1 CCRR : 2 CcRR : 1 ccRR : 2 CCRr : 4 CcRr : 2 ccRr : 1 CCrr : 2 Ccrr : 1 ccrr	9 Coloured : 7 Albinos

Table III gives the factorial details of these matings, showing how the above calculations have been made.

TABLE III. *Coloured × Albinos.*

Parents	Offspring	Result
(a) CCRR × (1) CCrr	All CCRR	All Coloured
(a) CCRR × (2) Ccrr	1 CCRr : 1 CcRr	All Coloured
(a) CCRR × (3) ccRR	All CcRR	All Coloured
(a) CCRR × (4) ccRr	1 CcRR : 1 CcRr	All Coloured
(a) CCRR × (5) ccrr	All CcRr	All Coloured
(b) CCRr × (1) CCrr	1 CCRr : 1 CCrr	1 Coloured : 1 Albino
(b) CCRr × (2) Ccrr	1 CCRr : 1 CCrr : 1 CcRr : 1 Ccrr	2 Coloured : 2 Albinos
(b) CCRr × (3) ccRR	1 CcRR : 1 CcRr	All Coloured
(b) CCRr × (4) ccRr	1 CcRR : 2 CcRr : 1 Ccrr	3 Coloured : 1 Albino
(b) CCRr × (5) ccrr	1 CcRr : 1 Ccrr	1 Coloured : 1 Albino
(c) CcRR × (1) CCrr	1 CCRr : 1 CcRr	All Coloured
(c) CcRR × (2) Ccrr	1 CCRr : 2 CcRr : 1 ccRr	3 Coloured : 1 Albino
(c) CcRR × (3) ccRR	1 CcRR : 1 ccRR	1 Coloured : 1 Albino
(c) CcRR × (4) ccRr	1 CcRR : 1 CcRr : 1 ccRR : 1 ccRr	2 Coloured : 2 Albinos
(c) CcRR × (5) ccrr	1 CcRr : 1 ccRr	1 Coloured : 1 Albino
(d) CcRr × (1) CCrr	1 CCRr : 1 CCrr : 1 CcRr : 1 Ccrr	2 Coloured : 2 Albinos
(d) CcRr × (2) Ccrr	1 CCRr : 1 CCrr : 2 CcRr : 2 Ccrr : 1 ccRr : 1 ccrr	3 Coloured : 5 Albinos
(d) CcRr × (3) ccRR	1 CcRR : 1 CcRr : 1 ccRR : 1 ccRr	2 Coloured : 2 Albinos
(d) CcRr × (4) ccRr	1 CcRR : 1 ccRR : 2 CcRr : 2 ccRr : 1 Ccrr : 1 ccrr	3 Coloured : 5 Albinos
(d) CcRr × (5) ccrr	1 CcRr : 1 Ccrr : 1 ccRr : 1 ccrr	1 Coloured : 3 Albinos

IDENTIFICATION OF INDIVIDUAL STUD PLANTS.

The practical consequences of these first principles are important and far-reaching from the Orchid breeder's point of view.

If each individual plant grown from a seed has a definite germinal constitution which determines its breeding powers and potentialities, then it is necessary that each individual plant used as a parent should have an identification mark. Whether this identification mark consists of an individual name, a stud number, or anything else is simply a matter of convenience, so long as the identity of each stud individual is maintained for future use. In 1909 (see p. 298) the writer suggested that identification might be assured by putting the name of the importer or raiser in brackets after the ordinary name together with a number showing the order of its appearance—*e.g.*, *Cypripedium callosum* Sanderæ [Sander I], [Low I], [Cookson I], [Statter I], and so forth. The first was imported in 1894, the second in 1904, and the third and fourth were raised by hand presumably from the first. All divisions of the original plant, as a rule, may be expected to have the same germinal constitution, and would consequently bear the same identification mark.

There is no doubt that in course of time certain individual plants would acquire a stud reputation much in the same way as a noted sire or brood mare does in thoroughbred horses, and the propagation of such an individual Orchid by division and its distribution would become a valuable economic asset.

Having secured the identification of each individual stud plant, the next step is to ascertain its germinal constitution by breeding from it. The original Mendelian method was to self the plant, but recent results show that this method alone is not sufficient to give a complete analysis of the germinal constitution of a plant. In order to do this it is necessary to cross-breed with it as a parent, and in cases like albinism, for instance, this is the only method possible. From this it is evident that the ordinary experiments in hybridisation and cross-breeding made by Orchid breeders are precisely what we require in order to ascertain the germinal constitution of individual plants, provided that each individual plant used as a parent is carefully identified for future reference and use.

SELF-STERILITY IN ORCHIDS.

The question of selfing Orchids leads us to another point which may be of some interest. Records of the flowering of seedlings from selfed hybrids are exceedingly rare in Orchids. At one time the author thought that this might be due, on the one hand, to the practical prejudice against in-breeding, or, on the other hand, to the idea that nothing new might be expected from selfing. Now, however, after attempting to self several hundreds of different flowers of *Cypripedium* and other Orchid hybrids at Burbage during the past ten years, the writer has come to the conclusion that self-sterility in hybrid Orchids has to be seriously reckoned with, being apparently the rule rather than the exception. For instance, since publishing my Mendelian experiments with *Cypripedium* \times *Hera* in 1903 (see pp. 99-108), I have from time to time endeavoured to self the individual F_2 hybrids as they flowered, but in every case but one when the capsules formed they afterwards proved to be empty. A few seeds, however, were secured from one capsule of selfed *C. \times Hera punctatum*, and a single F_3 plant has flowered which bred true to its spotted parent in so far as the spotted character was concerned.

On the other hand, Mr R. A. Rolfe¹ has obtained a number of seedlings at Kew of selfed *Epidendrum* \times *kewense*, several of which have flowered, and other odd records are to be found during the past twenty years, where selfed Orchid hybrids have produced plants which have flowered. These cases, however, appear to be exceptional.

In 1898 the writer (see p. 43) showed that sterility in hybrid *Cypripediums* was due in certain cases to a loss of power in the pollen of hybrids. For instance, species ♀ \times species ♂ produced 95 per cent. of fertile pods, while species ♀ \times hybrids ♂ gave only 56 per cent. Again, hybrids ♀ \times species ♂ produced 89 per cent., while hybrids ♀ \times hybrids ♂ gave only 59 per cent. It is possible that the same cause may be concerned in the self-sterility of Orchid hybrids generally, plus some other factor unknown.

Whatever difficulties may be met with in selfing hybrid Orchids, no such difficulty is apparently encountered in selfing certain species and varieties. I have found no special difficulty in raising seedlings of selfed species and varieties of *Cypripedium*, and many records are to

¹ Rolfe, R. A., "*Epidendrum* \times *kewense*: A Mendelian Experiment," *Orch. Rev.* xv. (1907), pp. 58, 59. [See also xvii. (1909), p. 69.]

be found in this and in other genera in Orchid literature¹. In view, however, of the great successes achieved by Orchid breeders in the hybridisation of diverse species and genera, it is hardly likely that selfing will be resorted to now to any great extent either in species or hybrids.

As we have seen, cross-breeding is a far more effective method of analysis than selfing, even from the point of view of Genetics. The crux of the whole problem, however, lies in the identification of individual plants. Unless this is done all the rest is vain. Unfortunately, with a few brilliant exceptions, our multitudinous Orchid records and labels are almost useless for this purpose. Some of these brilliant exceptions consist of certain unique hybrids to which their owners gave a distinctive name, proudly refusing to conform to the technical rules laid down by the authorities in nomenclature (and by the irony of fate the author happened to be one of the latter). Many of these names can be traced in *The Orchid Stud Book* as synonyms, and it is possible that the natural conservatism of Orchid breeders has caused them to retain many of these old names on their labels. If such is the case, the identification of some of our best stud individuals may not be so difficult after all.

In most cases, however, the adoption of genetic methods will necessitate the making over again of the best hybrids, using as parents the best *individuals* of the best varieties of the best species of the best genera. The primary hybrids thus obtained would be pedigree hybrids, and the best individuals of these might be further utilised in accordance with the particular aims that the breeder may have in view. In this way the Orchid breeder would be able to build up a pedigree strain made up of superior individuals, and the reversions and recombinations that he would obtain among the secondary hybrids would also tend to be superior to those bred in the ordinary way.

In breeding on these lines the Orchid breeder will soon discover for himself that while a few stud individuals may be homozygous, or pure for the good qualities required, the majority will be heterozygous, or impure for those particular characters. For stud purposes these impure forms should be discarded at once, no matter how good-looking they may be, and only the pure forms should be used for future breeding. Should the pure forms not turn up quickly enough for his purpose, the breeder can always make them from the impure forms in the ordinary Mendelian way. In many cases, no doubt, this will be well worth doing.

¹ Cf. the case of self-sterility in *Oncidium flexuosum* (p. 22).

This rigorous elimination of the impure plants that throw unwanted forms may sometimes require considerable courage on the part of the Orchid breeder, involving as it does the sacrifice of certain prejudices and predilections, especially when it comes to the point of discarding for stud purposes a much-prized plant that has perhaps won the classic F.C.C. at the R.H.S. The science of Genetics tells us plainly that things are not always what they seem, and a good-looking plant is not always a good plant to breed from. Only a few Derby winners are successful at the stud, everything depends on their germinal constitution. From the genetic point of view it would be a far sounder proposition to use for breeding an individual Orchid that had *bred* an F.C.C. winner than to use an actual winner of the F.C.C. that had a bad breeding record.

The F.C.C. awarded by the Orchid Committee of the R.H.S. is universally acknowledged to be the highest prize in the Orchid world, and winners of this prize may be regarded as classic Orchids. From the point of view of Genetics, the individual parents of these classic winners deserve special recognition as stud Orchids.

A reference to the records shows that during the past five years some 200 F.C.C.'s have been awarded by the Orchid Committee of the R.H.S. Of these F.C.C. winners about 150 appear to be hand-raised hybrids. Of the parents of these hybrids only 50 can be identified from the records as individual plants, and it is quite possible that a few of these names even may be represented in collections by more than one seedling individual.

Table IV gives a list of these classic stud Orchids, showing how many of their progeny have won the F.C.C. at the R.H.S. since November 1907. This short list is presented simply as an illustration for Orchid breeders of the potential value of certain stud Orchids, and there is no doubt that the list might be considerably extended with much advantage to the breeder.

May I venture to suggest that special groups made up of these stud Orchids and their progeny would provide an exhibit at the R.H.S. Shows that would not only be interesting to Orchid growers generally, but would be particularly useful to Orchid breeders as a demonstration of the germinal constitution of these stud Orchids? Competitive classes might even be arranged for these progeny tests to decide which individual Orchids are best for stud purposes.

The result would be to create a special demand for high-priced stud Orchids that hardly exists to-day. In view of the increasing number

TABLE IV. Classic Stud Orchids.

	Numbers of Progeny won F.C.C. at R.H.S. Nov. 1907—Nov. 1912.	
<i>Odontoglossum Rossii rubescens</i>	5	
<i>Cattleya Mossiae Wageneri</i>	3	(fig. 106)
<i>Cypripedium insigne Sanderæ</i>	3	(fig. 59)
<i>Cattleya intermedia alba</i>	2	(fig. 113)
<i>C. labiata alba</i>	2	(fig. 135)
<i>C. Trianae Imperator</i>	2	(fig. 138)
<i>C. Warscewiczii Fran Mélanie Beyrodt</i>	2	(fig. 137)
<i>Cypripedium</i> × <i>Hera Euryades</i>	2	
<i>C. insigne</i> <i>Harefield Hall</i>	2	
<i>C.</i> × <i>M. de Curte</i>	2	
<i>Lælia tenebrosa Walton Grange</i>	2	(fig. 136)
<i>Odontoglossum maculatum auriferum</i>	2	
<i>Calanthe</i> × <i>Sedeni burfordiensis</i>	1	
<i>C.</i> × <i>gigas Baron Schröder</i>	1	
<i>Cattleya</i> × <i>Fabia alba</i>	1	
<i>C.</i> × <i>Fabia Vigeriana</i>	1	
<i>C. Gaskelliana alba</i>	1	(figs. 108 and 134)
<i>C.</i> × <i>Hardyana alba</i>	1	
<i>C. Mossiae aurantiaca</i>	1	
<i>C. Mossiae Reineckiana</i>	1	
<i>C. Trianae Uplands</i>	1	
<i>Cypripedium aureum Œdippe</i>	1	(fig. 81)
<i>C. Harrisianum superbum</i>	1	
<i>C.</i> × <i>Hera Mariæ</i>	1	
<i>C.</i> × <i>Hera robustum</i>	1	
<i>C.</i> × <i>J. Howes</i>	1	
<i>C.</i> × <i>Leeanum giganteum</i>	1	
<i>C.</i> × <i>Leeanum Prospero</i>	1	
<i>C.</i> × <i>Milo Westonbirt</i>	1	
<i>C.</i> × <i>Minos Youngii</i>	1	
<i>C. Niobe Westonbirt</i>	1	
<i>C.</i> × <i>nitens magnificum</i>	1	
<i>C.</i> × <i>nitens Sanderi</i>	1	
<i>C.</i> × <i>nitens Salteri Hyeannum</i>	1	(fig. 77)
<i>C.</i> × <i>Thompsoni</i>	1	
<i>C.</i> × <i>Troilus</i>	1	
<i>Dendrobium nobile nobilitus</i>	1	
<i>Lælia anceps Schræderiana</i>	1	
<i>Læliocattleya</i> × <i>Hippolyta Phæbe</i>	1	
<i>Miltonia Bleucana Peetersii</i>	1	
<i>M. vexillaria Queen Alexandra</i>	1	
<i>Odontoglossum</i> × <i>Adrianæ F. K. Sander</i>	1	
<i>O.</i> × <i>amabile heatonense</i>	1	
<i>O.</i> × <i>amabile Royal George</i>	1	
<i>O. crispum Britannia</i>	1	
<i>O. crispum F. K. Sander</i>	1	
<i>O. crispum Graireanum</i>	1	
<i>O. Pescatorei Charlesworthii</i>	1	
<i>O.</i> × <i>Vuytsiekæ</i>	1	
<i>O.</i> × <i>Wilckeanum albens</i>	1	



Fig. 135. *Cattleya labiata* Lin.
(*Roy. H.*)



N.R.

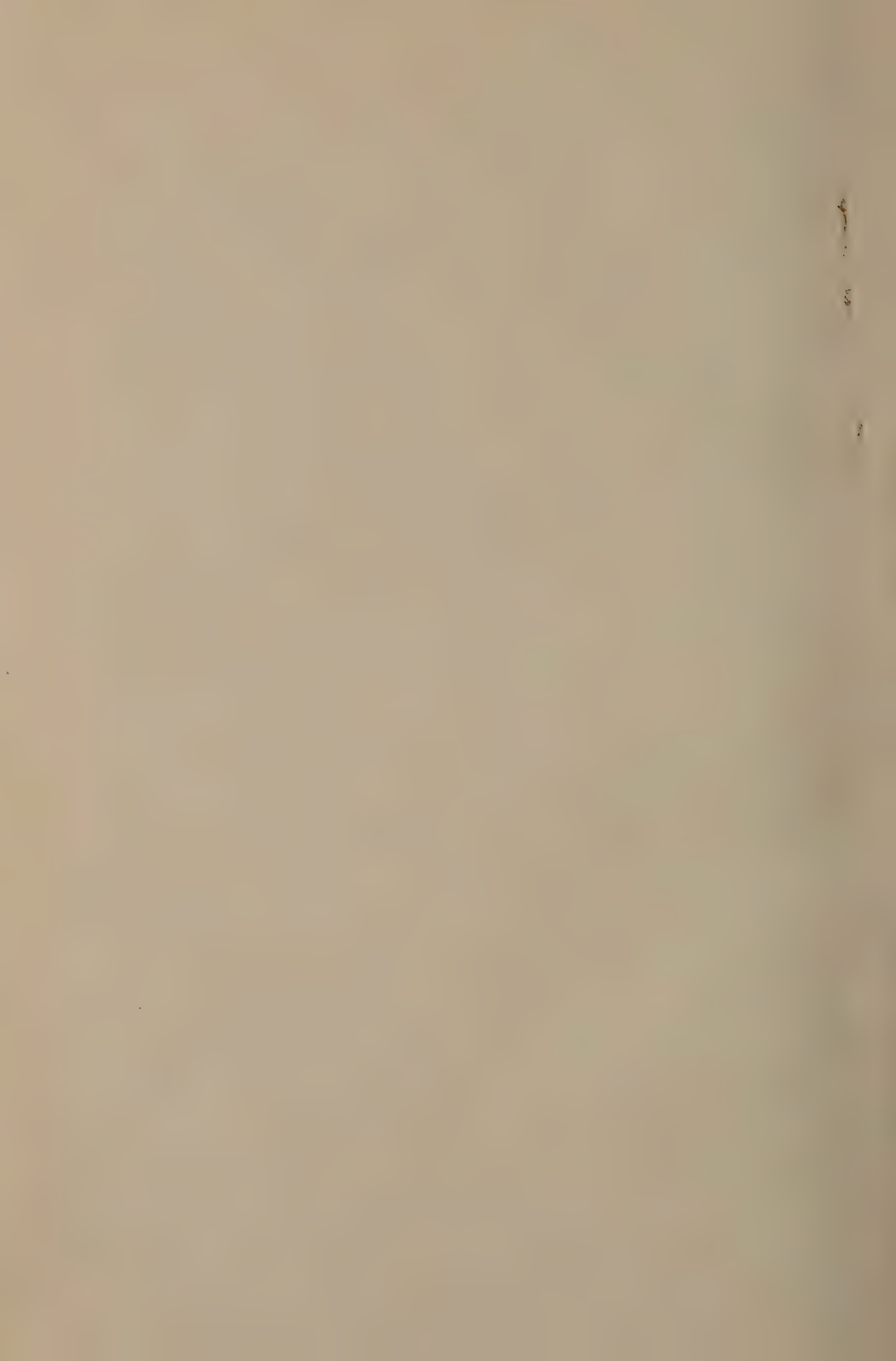




Fig. 136. *Lælia tenebrosa* Rolfe var. *Wal*
(*Roy.*





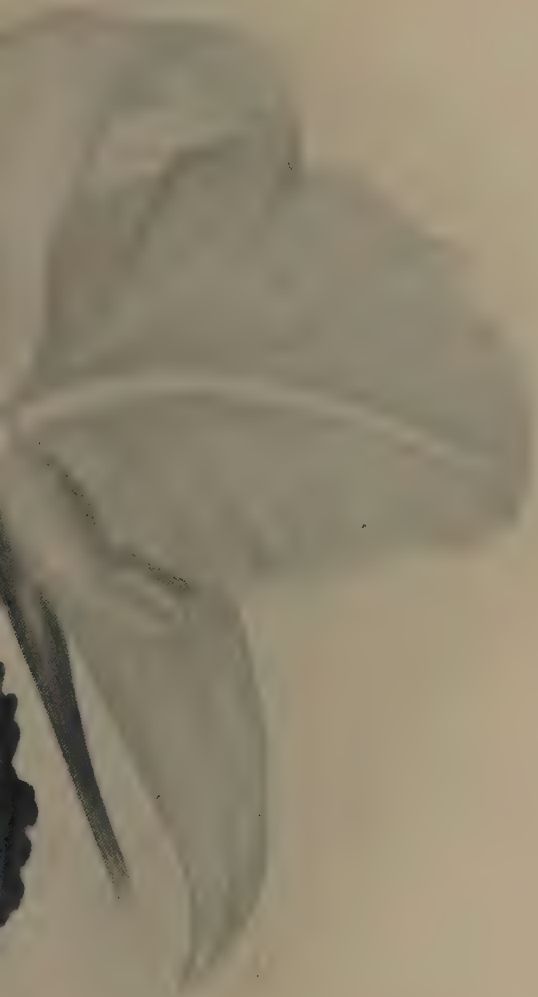
Fig. 137. *Cattleya Warscewiczii* Rehb. f. var. F
(Roy.)



Beyrodt Lambeau ex Cogn. Classic Stud Orchid.
(urn.)



Fig. 138. *Cattleya Trianae* Lind. et Rehb.
(*Rey.*)



erator Hort. Linden. A Classic Stud Orchid.
ourn.)

of Orchid-growers all over the world, it is hardly likely that such a demand would be confined to the British Isles, and there is no reason why this country should not in the future provide the world with stud Orchids, as it does to-day with thoroughbred horses and pedigree animals generally.

So far we have dealt with the general application of the principles of Genetics to Orchid breeding. It may be useful now to put the matter into a somewhat more concrete form by suggesting briefly a few special possibilities of the practical application of Genetics to Orchid breeding.

THE BREEDING OF ALBINOS.

The beauty and value of albino Orchids is generally recognised, and the Orchid breeder naturally wishes to raise new and improved forms by hybridisation. In other words, he wishes to vary the shape and size of the flower while retaining the chaste beauty of the albino. So far as we know, all albino Orchids breed true to albinism when selfed, but no remarkable improvement in shape, size, and distinctness can be obtained in this way. On the other hand, as we have already seen, when different species of albinos are crossed, they do not always breed true to albinism, but often give coloured forms, which are not wanted by the Orchid breeder.

The science of Genetics has provided a reasonable explanation of these interesting results. Experiments are yet wanting to provide breeders with a complete analysis of the germinal constitution of all the well-known albinos, and this cannot be satisfactorily accomplished until we can be quite certain as to the identification of individual albino plants, and, more important still, *that the albinos concerned are true albinos.*

Subject to the above reservations, the following list of twenty-six well-known albinos is given, with their presumed germinal constitutions so far as ascertained:

<i>Cypripedium callosum</i> Sanderæ	ccRR (fig. 101)
<i>C. Lawrenceanum</i> Hyeæ	ccRR (fig. 58)
<i>C. × Maudiae</i>	ccRR (fig. 102)
<i>C. insigne</i> Sanderianum	ccRR (fig. 103)
<i>C. × Rossettii</i>	ccRR (fig. 104)
<i>C. bellatulum</i> album	CCrr (fig. 105)
<i>Cattleya Mossiæ</i> Wageri	ccRR (fig. 106)
<i>C. Gaskelliana</i> alba	ccRR (figs. 108 and 134)
<i>C. × Hyeæ</i>	ccRR
<i>C. × Hyeæ</i> Suzanne	ccRR (fig. 107)

<i>C. × Hyeae Jungfrau</i>	ccRR
<i>C. intermedia alba</i>	ccRR (fig. 113)
<i>C. labiata alba</i>	ccRR (fig. 135)
<i>C. × Mackayi Dusseldorfei</i>	ccRR
<i>C. × Mackayi Undine</i>	ccRR (fig. 114)
<i>C. × Mackayi Westonbirt</i>	ccRR
<i>C. × Brenda</i>	ccRR
<i>C. × Peetersiae Myra</i>	ccRr (fig. 109)
<i>C. Harrisoniana alba</i>	CCrr (fig. 110)
<i>C. Mendelii alba</i>	CCrr
<i>C. Schroederæ alba</i>	CCrr (fig. 112)
<i>C. Warneri alba</i>	Ccrr (fig. 111)
<i>Dendrobium nobile virginale</i>	ccRR (fig. 115)
<i>D. Wardianum album</i>	CCrr
<i>Odontoglossum crispum xanthotes</i>	ccRR
<i>O. Pescatorei album</i>	ccRR

These albinos may be divided into two classes—C albinos and R albinos. To secure all albino offspring C albinos must be mated with C albinos, and R albinos with R albinos. If C albinos are mated with R albinos, coloured forms are bound to arise. The above list may serve a useful purpose as a provisional one for breeders to work upon, and no doubt further results in the near future will enable us to extend the analysis considerably, and also to confirm, or otherwise, the above tentative germinal constitutions.

In working with Albinos Orchid breeders must be careful to distinguish between true albinos and false albinos. True albinos have pure white flowers and green leaves, *without a trace of purple sap-colour*, though yellow and green plastids are usually present in the flowers. As we have seen, one or both of the colour factors C and R are absent from the germ-cells of these forms. On the other hand, false albinos, like *Cypripedium insigne Sanderæ*, *C. Lawrenceanum Gratrixianum*, *Cattleya Mossiæ Reineckiana*, and others, have a certain amount of purple sap-colour in the flowers and leaves, and consequently are not true albinos, though for practical purposes they are usually called "albinos," and in many cases are quite as beautiful and as much sought after as the true albinos. In these false albinos both the colour factors C and R are present, and consequently they give quite different results in breeding from the true albinos. These false albinos are really dilute coloured forms, and the fact that they usually behave as Mendelian recessives in breeding shows that their condition is due to the absence of a factor for dense or full coloration, which factor is present in the typical coloured form (cf. figs. 139 and 140).



Fig. 139. \times *Cypripedium Helena* Rolfe.
(*C. insigne* \varnothing (fig. 25) \times *C. bellatulum* σ (fig. 33).)
Showing Dense Coloration (CCRRDD). (*Orchid Review*.)



Fig. 140. \times *C Helena* var. *Armstrongia* Armstrong ex Rolfe.
(*C. insigne* *Sanderæ* \varnothing (fig. 59) \times *C. bellatulum album* σ (fig. 105).)
Showing Dilute Coloration (CcRdd). (*Orchid Review*.)



Fig. 141. \times *Odontoglossum percultum* (see fig. 144).

(The white form and the central flower above it represent respectively two of the individual grandparents
O. nobile and *O. crispum* Franz Masereel.)

(*Orchid Review*)

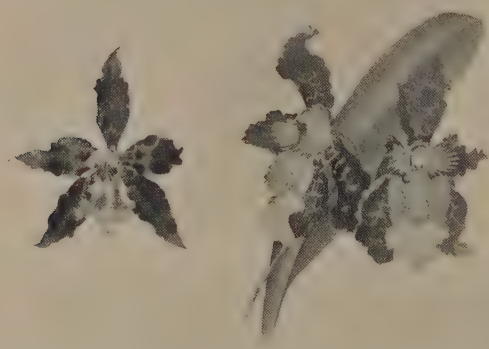


Fig. 142. *Odontoglossum*
luteopurpureum Lindl.

Fig. 143. *Odontoglossum*
Harryanum Rehb. f.

(Two ancestral species of \times *O. percultum*.)



Fig. 144. × *Odontoglossum percultum* Vuylsteke ex O'Brien. (See also fig. 141.)

Sixteen F_4 hybrids raised from one capsule by Mr H. J. Chapman. Four species are concerned in the pedigree—*O. crispum* Lindl. (fig. 141), *O. luteopurpureum* Lindl. (fig. 142), *O. nobile* Rchb. f. (fig. 141) and *O. Harryanum* Rchb. f. (fig. 143).

(*Orchid Review.*)

The different kinds of dilution found in most species suggest that more than one factor is concerned in the typical dense form. This application of Genetics to Orchid breeding explains a good many apparent mysteries. For instance, it explains why the false albino *Cypripedium insigne* Sanderæ breeds true to its special dilute form or throws true albinos when selfed, and yet behaves as if it were an ordinary *C. insigne* when crossed with the true albinos *C. × Maudiae*, *C. Lawrenceanum* Hyeaunum, and *C. callosum* Sanderæ. These true albinos arose originally by the loss of a colour factor (C), but the factor for dense coloration (D) would still be present in those albinos, though not manifested on account of the albinism. When this factor for dense coloration (D) is brought in by the cross, it naturally causes the parent *C. insigne* Sanderæ to behave as if it were an ordinary *C. insigne*.

If these so-called "reversionary" forms were to be self-fertilised or crossed *inter se*, both the recessive dilute coloration (dd) and the albinism (cc) would appear in certain individuals. On the average, the dilute forms would be expected to appear in three out of sixteen plants, and the albino forms in four out of sixteen plants. The recent cases reported in which the true albino *Cypripedium Lawrenceanum* Hyeaunum, crossed with the false albino *C. niveum*, gave typical coloured plants of *C. × Aphrodite*, and in which the false albino *C. niveum*, crossed with the false albino *C. Lawrenceanum* Gratianum, gave the false albino *C. × Aphrodite album*, are of course easily explained in the same way. To the student of Genetics such cases as these present no difficulty, as numbers of similar cases are well known in other plants and in animals.

THE RE-MAKING OF A BLOTCHED *CRISPUM*.

In 1909 (see p. 357) the author showed that the "blotched" character in *Odontoglossums* behaves as a Mendelian dominant to the "plain" character, which is recessive. Since then further evidence has given ample confirmation. The logical consequences of this application of Genetics to Orchid breeding lead one to support Mr de Barri Crawshay's idea, expressed many years ago, that blotched crispums first appeared in a wild state through natural hybridisation with other species.

From the point of view of Genetics, a dominant character is due to the addition of a factor, while a recessive character is due to the subtraction of a factor. A blotched *crispum* therefore consists in the addition of a factor to the ordinary typical plain *crispum*. The question arises, How was this dominant blotched character added to the typical

plain *crispum*! In order to illustrate the point we will take in hand the re-making of a blotched *crispum* by crossing an ordinary white plain *crispum* with one of the yellow blotched species that grows with *O. crispum* in Colombia—say, *O. luteopurpureum* (fig. 142); the result will be, of course, the F_1 yellow blotched hybrid known as *O. × Wilckeanum*¹, yellow being dominant to white, and blotched to plain. This natural hybrid appeared in importations before it was first raised in gardens.

Next we will re-cross this yellow blotched hybrid with another white plain *crispum*. The expected result, so far as these two characters are concerned, will be that in F_2 , out of four plants, we shall get on the average one yellow blotched, one yellow plain, one white blotched, and one white plain. Among the white blotched forms will be found blotched crispums. There can be little doubt that is how the blotched crispums originated in a wild state by natural hybridisation, e.g. *O. crispum Franz Masereel* (fig. 141).

Other crossings might, of course, give the blotched *crispum*, but it seems more likely that it should originate from this particular cross than any other on account of the natural distribution of these forms, as estimated by their frequency in importations (cf. figs. 141—144). Further confirmation may be found in the fact that so far all the imported blotched crispums that have been bred from have proved to be heterozygous, or impure to the blotched character, giving plain forms when mated together.

For instance, the blotched *O. crispum Franz Masereel*, *O. crispum Leonard Perfect*, *O. crispum Lindeni*, *O. crispum Victoria-Regina*, *O. crispum Rossendale*, *O. crispum Marie*, *O. crispum Luciana*, *O. crispum Crawshayanum*, and *O. crispum Alphonso* all give some plain forms when mated with blotched and plain forms, showing that each has only a single dose of the blotching factor (figs. 145—147). This indicates that one of their parents was a plain *crispum*, otherwise some homozygous blotched forms would surely have turned up amongst them.

The next step for Orchid breeders to take, therefore, is to breed these heterozygous, or impure, blotched forms *inter se*. On the average, one out of three of the blotched forms produced in this way should be homozygous, or pure, with a double dose of the blotching factor. These when bred from will give *all* blotched forms, whether mated with other blotched forms or with plain forms. The interesting blotched forms recently raised by Messrs W. Bull from *O. crispum Franz Masereel* × *O. crispum Alphonso* would provide excellent material for such an experiment (fig. 145).

¹ × *Odontoglossum Denisonae* Londesborough ex Rolfe et Hurst.



Fig. 145. Six seedlings out of the *Blotched Odontoglossum crispum* Lindl. var. *Alphonso* Bull ex Rolfe ♀
by the *Blotched* O. c. Franz Masereel Vervet ex Rolfe ♂ (fig. 141).
Showing Segregation of Plain from Blotched and the Recessive Nature of Plain.
(*Orchid Review*.)



Fig. 146. The *Blotched* *varianum*
 ♂ pa

Fig. 148 b. *O. c. Blotched* var. ♂.

Fig. 148 c. *O. c. Bonnyanum* Seedling.

(*Orchid Review*.)

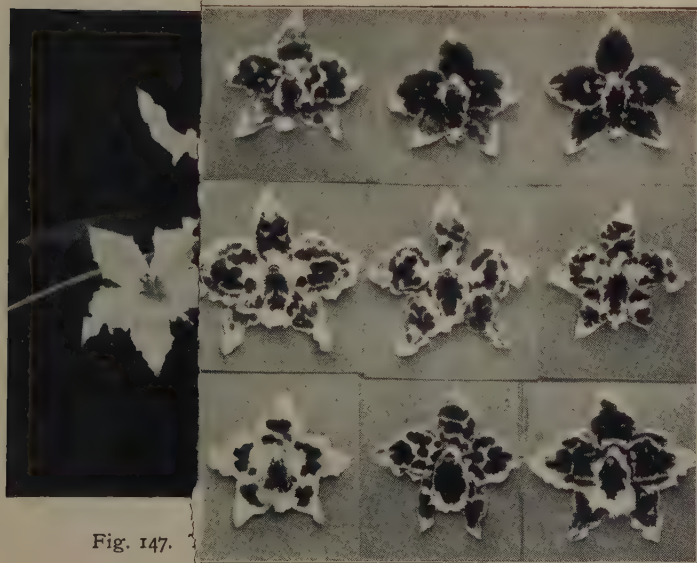


Fig. 147.

From the

1 Seedlings, showing range of variation in Blotching.

It will, of course, be understood that the blotched character in *Odontoglossums* is a very variable one, the blotches vary in size, form, and number, while the pattern varies with the species used (figs. 148 and 149). It would be an interesting study to work out the several factors that are no doubt concerned in the different kinds of blotching. The plain form of *O. crispum* is usually slightly spotted, especially on the lip. The yellow ground colour in *Odontoglossums* varies considerably in shade according to the species and variety used. Some of the bright yellow species are evidently heterozygous, or impure, carrying cream recessive, as may be seen in some of the F_1 results of yellow \times white in certain primary hybrids where segregation into the two distinct shades, cream and canary-yellow, is evident. When a pure white ground appears in F_1 results of yellow \times white, it is evidently due to the impure nature of the wild yellow form used as a parent.

THE MAKING OF A SCARLET *CRISPUM*.

A large number of interesting problems have already been taken in hand by Orchid breeders, some of which bid fair soon to be successful, though to the student of Genetics the results seem to be slow in coming to hand.

The question, for instance, of the making of a scarlet *crispum* by combining the scarlet self-colour of *Cochlioda Næzliana* with the large size of *Odontoglossum crispum*. The making of a scarlet *Cattleya* by combining the scarlet self-colour of *Sophranitis grandiflora* with the large size and broad segments of the species of the *labiata* group of *Cattleya*. The making of a yellow *Cattleya* by combining the yellow self-colour of *Lælia Cowanii* with the large size and broad segments of the *Cattleya*. These and other problems equally interesting to Orchid breeders are, judging by the results recently presented, now well on the way to a solution.

There is no doubt that the application of the principles of Genetics to these problems would not only help to hasten their solution, but would also save much wastage of mistaken matings. In the three particular problems noted above the first crossings in F_1 all show a more or less incomplete dominance, both of the desired colour and size characters. In other words, the *single* dose of each factor present in the primary hybrid gives a different result from the *double* dose of each factor present in the pure parents. Thus the *double* dose of the factor present in the *Cochlioda*, *Sophranitis*, and *Lælia* parents produces the scarlet or yellow colour to perfection, whereas the *single* dose of the

factor present in the primary hybrids reproduces the scarlet or yellow colour more or less imperfectly (cf. figs. 150 and 154).

The same thing happens in regard to the factor for size. The *double* dose of the factor present in the *Odontoglossum* and the *Cattleya* parents produces the large size desired, whereas the *single* dose of the factor present in the primary hybrids does not. The simple solution of the problem, therefore, lies in choosing the particular matings that will give a *double* dose of each of the two characters that the Orchid breeder wishes to combine, in these cases the scarlet or yellow colour and the large size. It is obvious that this can be done by mating two of the F_1 hybrids together, and if the case is a simple one, as it appears to be, the desired result should be secured in F_2 , on the average in one plant out of every sixteen raised of the cross $O. \times Vuylstekeae \times O. \times Bradshawiae$ (figs. 150 and 154).

From this it will be seen that the common practice of mating the primary hybrid back to one of its parents cannot be expected to succeed, because such a mating implies the presence of a *single* dose only of one of the two characters concerned. By such a mating one of the characters is secured by a *double* dose at the expense of the other, which can only have a *single* dose (see fig. 153). Further, the many attempts that have been made to secure the result by breeding from secondary and more complex hybrids only lead to unnecessary complications, because owing to segregation it is quite possible to lose the desired factor altogether in the second generation F_2 , and the securing of a double dose of it by means of such matings is a matter of considerable uncertainty, with the chances very much against the breeder.

In passing, it may perhaps be useful to point out that the common practice of analysing Orchid hybrids of complex parentage in terms of fractions of their parents and ancestors is to be deprecated. In Orchid literature we often see it stated, for instance, that a certain hybrid is made up of $\frac{1}{8}$ A, $\frac{1}{8}$ B, $\frac{1}{4}$ C, and $\frac{1}{2}$ D. In the modern light of Genetics such statements are not only misleading, but in most cases they must of necessity be erroneous. The simple fact of the segregation of characters in the second generation altogether upsets such a calculation. It is the *pedigree* that may be said to be so constituted, not the individual hybrid.

So far, we have dealt with the three particular problems by applying the principles of Genetics in a general way to enable the breeder to secure a definite result in the shortest possible time. Space will not allow one to deal with the interesting mass of minor details concerned



Fig. 150. \times *Odontioda Vuylstekeæ* Crawshay ex Rolfe,
with its parent species,

Fig. 151. *Odontoglossum*
nobile Rehb. ♀.

Fig. 152. *Cochlioda*
Noetzeliana Rolfe ♂.

First step towards a Scarlet *Crispum*.

(*Orchid Review*.)



Fig. 153. *Odontioda Vuylstekei*
(\times *Odontioda Vuylstekei*)
Ba

in these three problems. One or two special points however may be noted. Judging from the F_1 results recently produced it would appear that in order to get a true scarlet *crispum*, *Cochlioda Nætzliana* should be crossed with an *Odontoglossum* with a white ground colour—e.g., *O. crispum* or *O. nobile*; and in order to avoid, if possible, the presence of purple sap in the segments it would seem advisable to use the albino *O. crispum xanthotes* or *O. nobile album* in preference to the tinged, blotched, or plain forms, using, if possible, Charlesworth's individual R forms of these albinos, which breed true when crossed.

In order to get a crimson *crispum* it would appear that *Cochlioda Nætzliana* should be crossed with an *Odontoglossum* with a yellow ground—e.g., *O. triumphans* or *O. luteopurpureum*; and to avoid the dull purple tint in the crimson, the xanthic albinos *O. triumphans Ajax* and *O. luteopurpureum Vuylstekeanum* might perhaps be used to advantage. The presence of some purple sap in the column of *Cochlioda Nætzliana* may or may not complicate matters. It all depends whether the column colour is inherited independently of the rest of the flower or not; if a form can be secured in which the usual purple colour in the column is absent, this possible complication might be avoided.

In the making of a scarlet Cattleya the elimination of the rose-purple sap of the Cattleya is equally important in order to get the true colour, and it would therefore seem advisable to use with the *Sophronitis* the albino form—e.g., *Cattleya Mossiae Wageneri* and *C. Gaskelliana alba*. If the (C) albinos of *C. Warneri* and *C. Schröderæ* are used, care must be taken not to put them in the same experiment in which the (R) albinos of *C. Mossiae* and *C. Gaskelliana* are used, otherwise the sap-colour will appear.

In place of *Sophronitis grandiflora*, the species *Lælia harpophylla* or *L. cinnabarina* might be used, but the result would be a lighter and more orange shade of scarlet.

In the making of a self-yellow Cattleya, the species *Lælia Cowanii* or *L. flava* would appear to be the best to use. *C. Dowiana aurea* and *L. xanthina*, being bi-colors, would be unsuitable for breeding selfs. It is rather curious that, while the yellow colour of *C. Dowiana aurea* is completely recessive to the rose-purple colour of the Cattleyas, the yellow colours of *L. Cowanii*, *L. flava*, and *L. xanthina* are dominant, though in most cases the dominance is incomplete. The F_1 results suggest that the colour of the front lobe of the lip may be

inherited independently of the rest of the flower. The bi-colors *C. Dowiana* and *L. xanthina* give purple or crimson lips when mated with albinos, while *L. Cowanii* and *L. flava* apparently do not; but *L. flava* when mated with the coloured forms of certain species gives a crimson or purple lip, while with other species it gives a self-yellow flower. *L. Cowanii* so far appears to give all yellow selfs with both coloured and albino forms.

In the making of a self-yellow *Cattleya*, all these details will have to be carefully considered by the breeder in choosing his matings. It may be interesting to anticipate that a rather curious point will arise in the making of these scarlet and yellow *Cattleyas*. Technically, according to the present rules, the scarlet *Cattleyas* bred in the way suggested would belong to the genus \times *Sophrocattleya*, while the yellow *Cattleyas* would be classed as \times *Leliocattleya*. But, as the writer pointed out in 1904 (see p. 146), the generic characters which separate *Cattleya* from *Laelia*,—i.e. four pollinia and eight pollinia respectively—themselves behave as Mendelian characters, and segregate in F_2 in the same way that specific and varietal characters do. Consequently some of the scarlet and yellow *Cattleyas* raised in these experiments will have four pollinia only, and in that sense would be indistinguishable from the systematist's true *Cattleya*. Being homozygous, they would also breed true to that character. In view of this, it hardly seems logical to call them \times *Leliocattleya*; and if the Orchid breeder, for other reasons of his own, chooses to call these forms *Cattleyas*, in the circumstances it will be a rather difficult matter to deny him (e.g. see fig. 155).

ECONOMICS AND EUGENICS.

The application of the principles of Genetics to Orchid breeding brings out an economic point of considerable importance, the appreciation of which should save the breeder a considerable amount of time, trouble, and expense. From what we have shown, it is evident that no useful purpose can be served by the indiscriminate matings of complex hybrids, which are far too common in Orchid breeding. From the economic point of view, it is extremely doubtful whether it is really necessary to go beyond the mating of primary hybrids in Orchid breeding. We have seen that any two good qualities can be combined in this way in the second generation, in a single experiment with two three, or four species.



Fig. 155. \times *Læliocattleya Wiganiae* Wigan ex O'Brien.

(*Cattleya Mossiae* Hook φ \times (*Cattleya Warneri* Moore ex Warner φ \times *Lælia tenebrosa* Rolfe σ δ), with four Pollinia as in the genus *Cattleya* Lindl.

Eight Hybrids of this generic back-cross were flowered at Burbage: three had four equal Pollinia as in the genus *Cattleya* Lindl.; five had eight unequal Pollinia as in the hybrid genus *Læliocattleya* Rolfe; none had the eight equal Pollinia of the genus *Lælia* Lindl.

If more than this be required, other parallel experiments can be carried out at the same time, and the respective results of the separate experiments can, if really necessary, be combined afterwards. For instance, Experiment 1 might be carried out to make a dark scarlet *Cattleya* from *Sophranitis grandiflora*, while Experiment 2 might be carried out at the same time to make a light scarlet *Cattleya* from *Laelia harpophylla*. When these two shades of the scarlet *Cattleya* are obtained in the second generation, they might be mated together in order to produce in the third generation a scarlet *Cattleya* superior to both.

Another great advantage in the adoption of the method of parallel experiments would be that the special secondary hybrids obtained in this way will of necessity have a double dose of each of the two good qualities; consequently they will be equally valuable for use as stud Orchids, being homozygous, or pure to the desired characters, they will breed true to themselves when selfed, and will give more definite and less variable results when crossed with one another.

The application of the principles of Genetics to Orchid breeding leads one to conclude that, from the economic and eugenic points of view, the only sound method to adopt in Orchid breeding is to make a fresh start by selecting a choice stud of the best individuals of the best varieties of the best species of the best genera, due preference being given to those stud individuals that have already *bred* winners of the F.C.C. at the R.H.S., and have also proved themselves to be *homozygous* in their good qualities. These selected stud Orchids should be combined by crossing in every possible way, in order to make superior primary stud hybrids. Finally, these superior stud hybrids can be combined in any way that the breeder may think fit, in accordance with the particular objects he may have in view.

XXXIII

NOTES ON THE BURBAGE EXPERIMENTS IN GENETICS, 1913¹

(1) ON THE INHERITANCE OF MINUTE VARIATIONS IN GARDEN RACES OF *ANTIRRHINUM*.

For some years a series of investigations has been carried out here in order to ascertain the nature of the various "rogues" that constantly appear in the best horticultural stocks of Culinary Peas, Sweet Peas, and *Antirrhinums*. In the course of these experiments many thousands of single-plant cultures have been made, and incidentally some rather remarkable results have been witnessed concerning the inheritance of minute variations (fig. 156).

These minute variations, so uniformly and consistently inherited, comprise various tints, tones and shades of the same colour in flowers and foliage: minor grades of height and habit of growth: small differences in sizes and shapes of flowers: degrees of earliness and lateness of flowering or ripening of pods, together with other minute differences usually regarded as somatic fluctuations. These minute variations appear to follow ordinary Mendelian rules in their inheritance. As an illustration of the inheritance of these minute variations in various plants, a single case in *Antirrhinum* is presented.

The garden variety "Aurora" breeds true to its bushy and intermediate habit of growth, its scarlet lips and ivory tubes. Individual plants, however, show slight differences in habit, earliness, size and colour of flowers. These when bagged and selfed gave the following results:

(1) Three grades of habit were selected, Tall (No. 25), Medium (No. 16), and Dwarf (Nos. 26 and 27), and each plant bred true to its individual grade, while still retaining its bushy and intermediate habit.

¹ Printed for information on the occasion of the second visit of the members of Sects. D, K and M of the British Association to Burbage on Sept. 16th, 1913, at the Birmingham Meeting.



Fig. 156. View of *Antirrhinum* Experiments at Burbage,
Showing the methods used for isolating individual plants and Pure Lines.

(2) Three grades of earliness were selected, Early (No. 26), Medium (No. 16), and Late (Nos. 25 and 27), and each plant bred true to its individual grade.

(3) Three grades of flower-size were selected, Large (Nos. 25 and 27), Medium (No. 16), and Small (No. 26), and each plant bred true to its individual grade.

(4) Three grades of the scarlet flower-colour were selected, Dark (Nos. 16 and 25), Medium Dark (No. 27), and Light (No. 26). Each of the Light and Medium Dark plants bred true to its individual grade, while the Dark plants both showed segregation; No. 16 giving four grades, Dark, Medium Dark, Medium Light, and Light, and No. 25 three grades only, Dark, Medium Dark, and Medium Light.

The four grades of scarlet colour approximate closely to the following shades in the *Répertoire de Couleurs*, and apparently depend on the varying amounts of red sap present on the yellow ground colour. Dark = Rouge Cardinal (112): Medium Dark = Rouge Tomate (81): Medium Light = Rouge Feu (78): Light = Rouge Saturne (58).

These results together with others witnessed here in *Antirrhinums*, Sweet Peas, and Culinary Peas, seem to be significant, inasmuch as they show that many presumed unit-factors can be analysed into several sub-factors which themselves behave as units.

The question arises, are we to regard these sub-factors A_1 , A_2 , A_3 , as representing different states or powers of the original unit-factor A , or must we raise them to factorial rank B , C , D ?

In any case it is evident that these minutely continuous variations are strictly discontinuous in their inheritance.

If such phenomena prove to be general in plants and animals, they may throw some light on the question of the evolution of species by minute variations.

(2) THE SEGREGATION OF SPECIFIC CHARACTERS IN F_2 HYBRIDS OF *BERBERIS*.

× *Berberis stenophylla* (No. 3) is a garden hybrid between the distinct species *B. Darwinii* (No. 1) and *B. empetrifolia* (No. 2). Only a single seedling of this primary hybrid appears to have been raised, and it may be described as fairly intermediate between the parent species in all its characters.

About 3000 F_2 seedlings of this hybrid have been raised here (No. 4), and so extremely variable are they that it is rather difficult to find two

that are exactly alike. Very few are precisely like the hybrid parent, and not a single plant has yet been found with all the characters of either of the original species.

At the same time it is evident that segregation has taken place, since many of the specific characters of both *B. Darwinii* and *B. empetrifolia* have re-appeared in different individuals, apparently unchanged. The principal characters of the original species that seem to have segregated in F_2 are:

(1) *B. Darwinii*: Tall, upright habit: thick, much branched, hairy stems: five short, equal spines: broad, flat, light green leaves: racemose, orange-yellow flowers, with long, narrow segments and red pedicels.

(2) *B. empetrifolia*: Dwarf, prostrate habit: slender, little-branched, glabrous stems: three long, unequal spines: narrow, revolute, dark green, glaucous leaves: single or sub-umbellate, golden yellow flowers, with short, broad segments and green pedicels.

In view of the large number of characters concerned in these hybrids the chances of a true *B. Darwinii* or *B. empetrifolia* appearing are, of course, exceedingly remote. For with only six characters concerned the Mendelian expectation would be one plant in 4096, while with seven characters it would be one in 15,384, and so on.

Further experiments in F_3 are necessary to determine precisely the unit factors concerned in these hybrids, the segregation and various re-combinations of which have given rise to such an epidemic of variation.

These results may be useful to the Systematist as an example of what may be expected when natural hybrids seed with their own pollen. To the student of Genetics it is interesting to compare these complex specific hybrids of *Berberis* with the simple racial cultures of *Antirrhinum* noted above.

(3) BREEDING EXPERIMENTS WITH RACING PIGEONS.

During the past three years a number of racing pigeons of Belgian and English pedigree strains have been bred, trained, and raced in the National Races.

The primary object was to investigate the nature of the remarkable homing powers displayed by many racing pigeons, and to test how far, and in what manner, these powers may be transmitted to their offspring.

Naturally many years must elapse before a satisfactory answer can be given to either of these questions. It is already evident, however,



Fig. 157. Fixed Loft for Racing Pigeons.
Used in the experiments at Burbage.



Fig. 158. Primitive Mobile Pigeon-Loft.
Used for experiments at Burbage before the War.



Fig. 159. Pons Mealy Hen.

Bred from Pen A out of No. 1 Red-chequered Hen by No. 2 Red-chequered Cock (fig. 160).



Fig. 160. No. 1, Red-chequered Hen, dam of Nos. 3—6 and fig. 159.
 No. 2, Red-chequered Cock, sire of Nos. 3—6 and fig. 159.
 No. 3, Marennnes Mealy Hen.

that the popular idea that the birds home solely by instinct must be considerably modified if not altogether abandoned. Intelligence rather than instinct seems to be the main factor which determines a bird's homing and racing ability.

Results show that incompetent or feeble-minded pigeons may be bred from competent or intelligent parents, and it is interesting to find that feeble-mindedness behaves as a recessive character in birds as well as in Man.

Fortunately, or unfortunately, it is much more difficult to get offspring from the feeble-minded in Pigeons than in Man.

The following notes will illustrate the progress of the work that is being carried out here:

In 1911—12 twenty pairs of pedigree Stock produced 64 birds that were trained and raced on the South Road. Of these, 36 flew up to the Coast as young birds (either to Bournemouth 126 miles or Ventnor 134 miles), and 28 failed.

As yearlings, 15 of the surviving 36 flew across the English Channel (either from Jersey 234 miles, or Rennes 306 miles), and 21 failed.

Next year, as two year olds, the 15 survivors will be sent on to Nantes 368 miles, Marennes 463 miles, or Bordeaux 534 miles¹.

It is interesting to observe that out of the 15 birds that flew the Channel as yearlings, 5 were bred from one pair (Pen A).

This suggests that homing ability may be inherited. Further it is rather remarkable that 3 out of the 5 Channel birds bred from this pair are Mealy hens (figs. 159 and 160 No. 3). Both the parents are Red Chequers (Pen A) (fig. 160 Nos. 1 and 2), and have produced so far 16 Red Chequers to 4 Mealies (which incidentally shows the recessive nature of the Mealy colour, presence of Chequering being dominant and absence recessive, extracted Mealies bred together so far having given Mealies only).

The other Mealy bred from the pair was a cock, which failed to fly the Channel (fig. 160 No. 6). On the other hand the only Chequered cock that was raced, flew the Channel, while of five Chequered hens raced, one flew the Channel and four failed¹.

The above numbers are of course too small to give smooth results, and further experiments are necessary to ascertain whether, in the case of this pair, there is any sort of tripling or linkage of homing ability with Mealy colour and female sex¹.

¹ In 1914 only two birds returned from the long races from Pons 484 miles and Marennes and both were Mealy hens bred from Pen A (figs. 159 and 160 No. 3). (Note added 1924.)

The large excess of females so far produced by this pair—13 females to 3 males—seems noteworthy, especially in regard to the distribution of the sexes in the three seasons' breeding. In 1911 the proportion was four females to three males. In 1912 there were five females and no males. In 1913 there are apparently four females and no males. It should be stated, however, that in 1912 and 1913 three eggs were infertile, and four squeakers were lost from the loft before their sex could be ascertained.

The distribution of the Mealy and Chequered colours in the three seasons was less irregular. In 1911 there were five Chequers and two Mealies. In 1912 precisely the same. In 1913 there are six Chequers and no Mealies.

The normal expectation is of course a Mendelian distribution, on the average, of three Chequers to one Mealy, with equal numbers of Males and Females.

(4) BREEDING EXPERIMENTS WITH DUTCH RABBITS.

A general investigation concerning the inheritance of Coat-Colour in Rabbits has been made here during the past 11 years, but recently special attention has been given to the questions of the inheritance of the variable Dutch markings, and of the different shades of each of the four standard colours in Exhibition Dutch, viz.: Black, Blue, Steel-Grey and Tortoiseshell.

Dutch Markings: Results show that the low grade markings classed as Grades 1—3 (spotted coat) (fig. 161) have a discontinuous inheritance from the high grade markings 4—9, behaving as simple recessives. (The standard markings are Grade 5 (figs. 162, 163 and 164).) Consequently the low grades can be altogether eliminated from the stud by the selection of homozygous standard grades which throw no spotted wasters¹. In order to apply this knowledge several well known winners and pedigree animals have been purchased from the leading exhibitors and breeders of Dutch, and have been gametically tested, with the following results, *e.g.*: Ch. Blue Laddie, Ch. Master Magpie, Black Cap, Blackburn Black, Leicester Tortoise (No. 27) and Derby Steel (No. 28) have all proved to be heterozygous dominants carrying the low grade spotted recessive. On the other hand, *e.g.*, Ch. Mikado (No. 29) (fig. 163), Yorkshire Bobby (No. 25), and Bristol Steel (No. 26) have proved to be

¹ By crossing Standard Dutch of Grade 5 with English-marked (fig. 96) I have found that Grade 9 also behaves as an unit-character *recessive* to Standard Grade 5, which further simplifies the problem of breeding Dutch to Standard markings. (*Note added 1924.*)



Fig. 161. Low Grade or Spotted Dutch of Grade 2.



Fig. 162. Heterozygous High Grade (5) Standard Dutch,
Carrying Low Grade or Spotted Dutch Recessive.

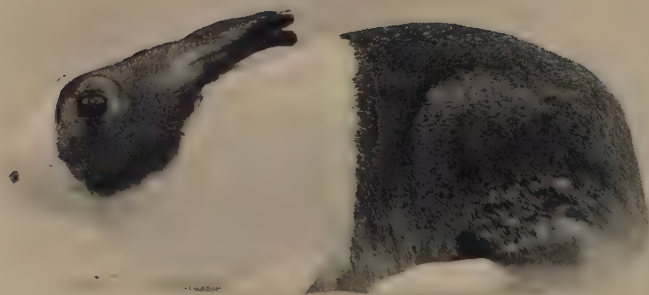


Fig. 163. Ch. Mikado Steel-Grey Buck.

A Homozygous High Grade Standard Dutch which threw no Low Grade Spotted Dutch.



Fig. 164. Ch. Burbage Yellow Premier.

The First Champion Yellow Dutch produced.

Bred at Burbage.

homozygous dominants which throw no spotted wasters however mated. Thus a homozygous line of Dutch has been established, from which the spotted defectives have been altogether eliminated, a result which at all events is a step towards the easier breeding of a Champion Dutch Rabbit, a task which is perhaps the most difficult that any breeder can undertake¹.

Colour Breeding: The principal Mendelian factors that determine Coat-Colour in Rabbits have already been ascertained by the experiments of Castle, Punnett and the author, but the practical question of how to breed the correct shades of each colour for exhibition requires considerable and minute investigation, and some years must elapse before any definite and satisfactory scheme can be presented. Some progress has however been made; for instance, it is already evident that the best shade of Black for show purposes is a heterozygous form carrying Blue recessive, the homozygous Black and the heterozygous Black carrying Tortoiseshell being apparently too rusty for exhibition. Similarly the Exhibition Steel-Grey (Nos. 28 and 29), which is a light shade of Black-Agouti, is probably always heterozygous for blue. Consequently winning Blacks and Steels cannot be expected to breed true to colour, and winners must be re-made every time by special colour matings.

In the process of breeding Steels a number of "off colours" such as blue-grey, pale-grey (Wild Agouti), and dark steel (Agouti-black), (No. 30), naturally arise, and the best one can do is to reduce these to a minimum by a discriminating use of the knowledge of the Mendelian factors concerned in the inheritance of colour.

(5) BREEDING EXPERIMENTS WITH UTILITY POULTRY.

Various breeding experiments with Poultry have been carried out here since 1900, but in 1910 a new series of experiments was devised in order to investigate the inheritance of certain economic qualities.

Attention has been mainly directed to the questions of the inheritance of Egg-Yield, Egg-Size, and Egg-Colour, in Utility White Leghorns and White Wyandottes. So far 134 pullets have been reared of the two breeds and their F₁ cross-breds. Each individual bird has been separately housed (fig. 165) and records taken of the number, size, and colour of her eggs during the first twelve months of laying.

¹ Ch. Burbage Yellow Premier (fig. 164), the first Champion Yellow Dutch Rabbit produced, was bred at Burbage on the above principles in two years. (*Note added 1924.*)

During the progress of the experiments an important paper has been published by Dr Raymond Pearl on his experiments in the inheritance of fecundity in Plymouth Rocks and Indian Game fowls in America.

Pearl concludes that a high Egg-Yield is due to the presence of a certain Mendelian factor representing a high Winter-Yield. Further he finds that this factor is sex-linked in its inheritance so that a hen never inherits her high Egg-Yield through her dam but always through her sire.

The Burbage experiments are not yet sufficiently advanced to fully test Pearl's hypothesis (in so far as it can be applied to the different material used) (see pp. 468—521).

In order to illustrate the nature of the work that is being carried out, a single case is presented:

No. 10. A pedigree White Wyandotte Cock (W. P. F.).

No. 5. A pedigree White Leghorn Hen (Cam and Padman).

Nos. 48—55¹. Seven F₁ hens bred from the above pair.

(1) *Egg-Yield*: The ♀ parent laid 178 eggs in her first year. Two sisters of the ♂ parent laid 179 and 126 respectively. The F₁ cross-breeds laid in their first year as follows: No. 54 = 215; No. 49 = 202; No. 48 = 201; No. 53 = 180; No. 55 = 177; No. 51 = 168; No. 50 = 144.

Owing to the fact that these seven hens were hatched in January and began to lay in June, it is difficult to estimate their winter record satisfactorily according to Pearl's method. For if all the eggs laid before March 1st be taken as the basis the result will be certainly too high, while on the other hand, if the number of eggs laid between Nov. 1st and March 1st be taken, the result will be necessarily too low (see p. 479).

(2) *Egg-Size*: The Weight-Mode of the eggs laid by the ♀ parent was 56.5 grams (Grade 5). Both the sisters of the ♂ parent had a W.M. of 49.5 grams (Grade 3). The W.M.s of the eggs laid by the F₁ cross-breeds were as follows: Nos. 48, 51 and 54 each had a W.M. of 53 grams (Grade 4): No. 53 had a W.M. of 49.5 grams (Grade 3): Nos. 49, 50 and 55 each had a W.M. of 46 grams (Grade 2).

These results, together with others, suggest that both the ♂ and ♀ parents transmit to their daughters factors for Egg-Size, and that the smaller grade egg is dominant to the larger grade (see p. 496).

(3) *Egg-Colour*: The Colour-Mode of the eggs laid by the ♀ parent was a Tinted White (Grade 1). The C.M.s of the eggs laid by the two sisters of the ♂ parent were Light Brown (Grade 3): and Brown (Grade 4) respectively.

¹ No. 52 died young.

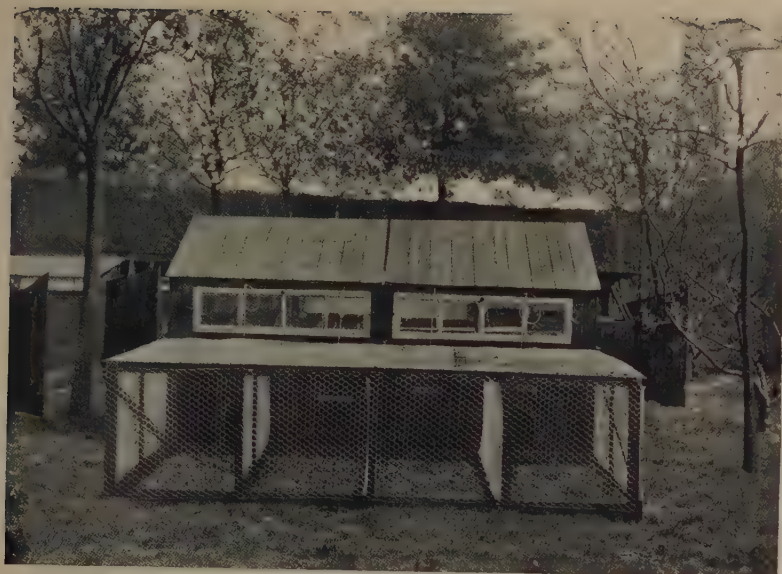


Fig. 165. Front and Side Views of Movable Poultry Houses

Used in the experiments at Burbage, each housing four hens with separate nests, roosts and runs.

The C.M.s of the eggs laid by the F_1 cross-breds were as follows: Nos. 51 and 54 each had a C.M. of Light Brown (Grade 3): the remaining five had each a C.M. of Cream White (Grade 2).

These results, together with others, suggest that both the ♂ and ♀ parents transmit to their daughters factors for Egg-colour, and that the darker tint of egg is dominant to the lighter tint (see p. 500).

(4) *Plumage Colour*: Both parents are pedigree Whites, while all the cross-breds show some traces of colour. Nos. 48 and 55 show traces of black pigment but would ordinarily pass for "Whites," while the remaining five are more or less coloured with buff and brown on a White ground. The precise significance of these results is not yet clear, but together with others, they show that one at least of the pedigree White parents is a heterozygous dominant carrying recessive or hypostatic colour (cf. expts. of Bateson and Punnett and see p. 214 *et seq.*).

(5) *Comb*: The ♂ parent is a pedigree Rose Comb, and the ♀ parent a pedigree Single Comb. Of the cross-breds Nos. 49, 53 and 55 have Rose Combs, while the remaining four have Single Combs.

These results, together with others, show that the ♂ parent is a heterozygous dominant, the factor for Rose Comb being present in some of his gametes and absent in others. The fact that all the Single Combs produced are smaller than the Leghorn comb of the ♀ parent suggest that the Rose Comb of the ♂ parent is based on a Single Comb of the Rock type. This may also possibly explain the distinct differences in shape between the Rose Comb of the ♂ parent and the Rose Combs of the F_1 cross-breds.

(6) *Size and Shape*: In build and feathering the F_1 cross-breds all appear to be more or less intermediate between the Heavy ♂ parent and the Light ♀ parent.

(7) *Disposition*: In all the cross-breds the quick temperament and wild disposition of the ♀ parent appears to be completely dominant to the slow temperament and tame disposition of the ♂ parent.

(8) *Broodiness*: The ♀ parent has never shown any signs of broodiness. The two sisters of the ♂ parent both went broody. Of the cross-breds Nos. 49, 50 and 53 have gone broody, while the remaining four have not shown any signs of broodiness. These results, together with others, suggest that the ♂ parent is a heterozygous dominant, the factor for broodiness being present in some of his gametes and absent in others (see p. 490).

(6) BREEDING EXPERIMENTS WITH HORSES.

Three sets of experiments in Hunter Breeding are being carried out, but naturally some years must elapse before any definite results can be expected.

(1) The mating of four Thoroughbred Mares of the homozygous 'Chaser line (reported to the Portsmouth meeting of the British Association in 1911) with selected Thoroughbred Stallions that have thrown good 'Chasers (see pp. 374 and 412).

From these matings four foals have been bred in the last two years, these will be put into training when fit, and duly tested on the Racecourse¹ (see figs. 131 and 132).

(2) The ordinary method of mating Half-bred Mares with a Thoroughbred Stallion of the Hunter type.

For this purpose the King's Premium Thoroughbred Stallion, "Denis Richard" (fig. 166), has been purchased, and was travelled in the district during 1912, serving 64 mares. This season he stood at home and served 43 mares.

The foals bred in this way will, with their dams, be kept under observation, and their future careers followed as far as possible¹.

(3) The mating of a pure-bred Shire Mare (fig. 167) with the Thoroughbred Stallion "Denis Richard" (fig. 166). A Chestnut colt foal (fig. 168) has been bred this season from this mating. This foal provides an illustration of the recessive nature of Chestnut coat-colour in horses (as reported to the Royal Society in 1905 (see p. 239)). It is evident that the Brown Shire Mare is a heterozygous dominant carrying Chestnut recessive, and it is probable from this result and others, that the Liver or Dark Chestnut Colour of the sire also behaves as a dominant to ordinary light Chestnut.

It is interesting to note the large increase of White in the face and leg markings of the foal as compared with the corresponding areas in the dam and sire (cf. figs. 166-168).

¹ Unfortunately owing to the War this has not been possible. (*Note added 1924.*)



Fig. 166. King's Premium Thoroughbred Dark Chestnut Stallion "Denis Richard,"
By "Laveno" out of "Millpond" (sire of fig. 168).



Fig. 167. Pure-bred Brown Shire Mare
(Dam of fig. 168).



Fig. 168. Light Chestnut Colt Foal,
Out of Brown Shire Mare (fig. 167) by Dark Chestnut Thoroughbred (fig. 166).

XXXIV

THE GENETICS OF EGG-PRODUCTION IN POULTRY¹

Six years' experimental breeding and testing on Mendelian lines, from 1910—16, with three distinct utility strains of White Leghorns and White Wyandottes, show that the first year's egg-production of a hen depends on the combined action of at least seven main genetic factors. The Mendelian pairs identified are:

E — e	Early — Late	Sexual maturity of pullets
W — w	Fast — Slow	Rate of winter production
S — s	Fast — Slow	Rate of spring production
M — m	Slow — Fast	Rate of autumn production
H — h	Broody — Non-broody	Instinct
N — n	Small — Large	Egg-mode
C — c	Brown — White	Egg-mode

The first of each pair is dominant, and the second recessive. In the course of the experiments more than 50,000 eggs were recorded and each egg was weighed and graded for size and colour. In order to analyse the complex and continuous data of egg-production a system of uniform gradings was formulated which ultimately led to the identification of the factorial pairs. The somatic gradings are based throughout on the genetic factors concerned, so that each hen has its somatic and genetic characteristics combined in a single formula. Production is graded in percentages.

Summary of the Results in White Leghorns and White Wyandottes.

Characters	Totals	Dominant	Observed	Calculated	Recessive	Observed	Calculated
Sexual maturity	335	Early (E)	286	289·00	Late (e)...	49	46·00
Winter rate ...	266	Fast (W)...	231	231·75	Slow (w)	35	34·25
Spring rate ...	224	Fast (S) ...	216	217·25	Slow (s)...	8	6·75
Autumn rate...	194	Slow (M)...	140	145·50	Fast (m)	54	48·50
Broodiness ...	201	Broody (H)	50	58·50	Non-B. (h)	151	142·50
Egg-size ...	331	Small (N)	135	128·75	Large (n)	196	202·25
Egg-colour ...	331	Brown (C)	137	142·00	White (c)	194	189·00
Totals... ..	1882	—	1195	1212·75	—	687	669·25

¹ Read before Section M at the Edinburgh meeting of the British Association for the advancement of Science, September 13, 1921.

Eighteen definite exceptions appeared, of which two proved to be somatic and not genetic, eleven were slight exceptions probably of the same nature, three were pathological, one was possibly an incomplete dominant, while one was apparently a true mutation.

Pearl's discovery of two genetic factors for winter production in Plymouth Rocks (1912), confirmed by Goodale in Rhode Island Reds (1918—19), is also confirmed in White Leghorns and White Wyandottes, in which the presence of both E and W factors is necessary for high winter-production.

No sex-linkage was found in either of the production factors of the Leghorns or Wyandottes used, and in this respect these two breeds resemble Goodale's Rhode Island Reds rather than Pearl's Plymouth Rocks (cf. p. 508).

There is a definite difference of rhythm between the discontinuous Slow (w) and the discontinuous Slow (s) birds, and it is possible that the Slow (s) birds are pathological.

Slow (M) birds are deep autumn moulters, while Fast (m) birds are partial autumn moulters.

A sensible proportion of broody hens do not show broodiness until their second season, so that it was not possible to ascertain in all cases the true nature of the "Non-Broodies."

The appearance of a few broody exceptions in the Leghorns gives support to Punnett's (1920) suggestion of the possible presence of an inhibitor to the broody factor in certain non-broody birds, and an H1 scheme of broodiness does bring into line many of the complicated and conflicting data published. To demonstrate this satisfactorily, experiments on a considerable scale would be required.

The results indicate the gradual evolution of the increase of fecundity in the hen by a succession of definite and discontinuous steps or mutations. Early maturity, fast winter rate, fast spring rate, and possibly brown-egg are dominant mutations, while fast autumn rate, large-egg, and possibly non-broodiness are recessive mutations. A single case of the occurrence of a recessive mutation for large-egg was observed, which originated in a Wyandotte cock. The experimental matings made were not suitable for testing satisfactorily the question of linkages of the above factors.

Economic Significance of Results. Pure and permanent strains of high producers of large eggs can be made by the elimination of birds carrying e w s M H N factors in accordance with the factorial scheme presented. E W S m h n birds are the best layers, and E E W W S S m m h h n n birds breed true. Results show that high production is not

incompatible with high fertility and vigour, as is often supposed. Old methods of grading production by winter and annual records are inadequate somatically, and misleading genetically. All things are possible to a winter-record in early hatchings.

The system of grading production presented has a double value to the practical breeder, because the descriptive somatic gradings, being based on the genetic factors concerned, give a line also to the breeding value of the bird, for the extreme grades tend to breed true. The grading of winter production by percentages minimises the unequal influences of variable dates of hatching. The adoption of this grading system to laying competitions would lead to rapid progress in poultry-breeding, and be of educational value to poultry-keepers in general, for the winning birds would breed winners with more frequency than they do now, and the reasons would be obvious. An extension of the laying competitions to 56 weeks or 400 days would extend the biological year of the layer to fourteen lunar months, and thus eliminate the deep moults (M birds). The result would be that the 200-egg hen would soon be superseded by the 300-egg hen.

Brown or white egg-mode can be bred true, and broodiness can no doubt be eliminated eventually by extended progeny-tests. The large egg-mode, which is so important in the Wyandotte, can be bred true by the elimination of the N birds of both sexes. The practical proof of the above scheme lies in the fact that homozygous strains of E E W W S S m m n n c c birds were bred in 1914 at Burbage from the heterozygous birds of the original pedigree strains.

Since the War (1919—21) other pedigree strains and other breeds have been tested with success on the basis of the above factorial scheme.

THE GENETICS OF EGG-PRODUCTION IN WHITE LEGHORNS AND WHITE WYANDOTTES¹

(1) INTRODUCTION.

EGG-PRODUCTION, FECUNDITY AND FERTILITY.

The term "Egg-production" is used in this report to denote the ability of a hen to form and separate from the body mature germ-cells or eggs. It is used in preference to the term "fecundity" for two reasons: First, because "fecundity" applies equally to the production of sperms by the male bird as well as the production of eggs by the female bird. (See Pearl and Surface 1909, and Pearl 1912.)

In these experiments we are concerned only with the egg-production of the hen, for at present we have no means of measuring the sperm production of the cock, and, therefore, do not know whether the cock which carries the genetic factors for high egg-production is actually a high producer of sperms or not.

In the circumstances, therefore, it seems preferable to use the term "egg-production" rather than "fecundity." Second, "fecundity" refers particularly to number-production, while egg-production may be extended to cover egg-size and egg-colour, as well as egg-number.

On the other hand, the term "fertility," as Pearl and Surface suggested in 1909, should be used to designate the total actual reproductive capacity of *pairs of organisms*, male and female, as expressed by their

¹ Reported to the National Utility Poultry Society, July 20, 1921, and reprinted from *The National Poultry Journal*, September 2 to December 9, 1921.

(From 1913 to 1916 the experiments were carried out with the assistance of grants from the Development Commission Fund, administered by the Ministry of Agriculture, through the National Utility Poultry Society.

I desire to acknowledge my indebtedness to Sir Daniel Hall, K.C.B., F.R.S., for without his encouraging support in 1913 the experiments could not have been carried on, and without his timely representations to the War Office in 1919 the Report could not have been presented in 1921.

My thanks are also due to Mr B. W. Horne and Mr T. R. Robinson, of the National Utility Poultry Society, for much practical assistance in the experiments; and last, but not least, to Mr J. B. Perkins, who faithfully devoted his whole time to the daily records of the experiments. C. C. H.)

An abstract of the above was read at the First World's Poultry Congress at The Hague, September 5, 1921.

ability when mated together to produce (or bring to birth) individual offspring.

Genetics is the science of experimental breeding on Mendelian lines. Mendelism and Mendel's laws of the segregation and assortment of the genetic factors in the germ-cells are now too well known to need introduction. If, however, there are any readers still unfamiliar with the elements of Mendelism, there is a simple account in Hurst (1907) (p. 265), and I would also recommend them to study at first hand Professor Punnett's more recent book on Mendelism (1919), which provides a sound introduction to the subject, and is cast in a popular form.

For more advanced students there is Professor Bateson's classic work on *Mendel's Principles of Heredity* (1913), and those who wish to learn the latest American developments of the chromosome theory of Mendelian heredity should study Professor Morgan's book on *The Physical Basis of Heredity* (1919).

Mendelism first saw the light in 1900, when Mendel's original and epoch-making contribution of 1865, on his experiments in crossing various races of garden peas, was rediscovered by three Continental botanists simultaneously and independently. (See Bateson, 1913.) From Mendel's little paper on garden peas a vast literature has come into existence (the titles alone of which would now fill a volume) clearly demonstrating the application of Mendel's laws of heredity to all kinds of plants and animals, including Man himself.

Mendel's laws have provided us with new and precise methods of analysis of the contents of the germ-cells by direct experiment, and a new and true science of heredity has been evolved, which in 1906 was named Genetics by Professor Bateson, the original leader of English Mendelians. Poultry fanciers will be proud when they realise the great part that their birds have played in the building up of Mendelism and the science of Genetics. The poultry experiments of Professors Bateson, Punnett, and Lippincott, Drs Davenport, Pearl, Goodale and Hadley, Major Bailey and the author, have all served to this end; and the useful conception of "presence and absence" in the development of Mendelism originated through the results of breeding the various kinds of fowls' combs together in our English experiments.

Burbage Experiments. From 1901 to 1908 Mendelian experiments with poultry dealt mainly with the investigation of superficial characters, such as down and plumage colour and comb form, most of which proved to be of a discontinuous nature, almost unaffected by external conditions, and consequently fairly simple in their genetics.

In 1910 experiments were undertaken by the author at Burbage, Leicestershire, to investigate the genetics of egg-production in utility poultry. This proved to be a most complicated problem, involving, as it does, a deep-seated physiological character of a continuous nature, fundamentally different from the superficial morphological characters of plumage colour and comb form previously investigated. The problem was further complicated by the serious difficulties met with in the variable influences of the external conditions on egg-production. From the outset it was evident that the genetics of egg-production was only a part of the general problem.

External Conditions. Egg-production is dependent on external conditions as well as internal genetic factors, on nurture as well as nature. External conditions, *e.g.* food, housing, exercise, climate, care and date of hatching, though vitally important to egg-production, are not dealt with here, but they have not been disregarded in the experiments. At an early stage certain uniform methods were adopted to place all individuals on an equal footing, so far as it was found possible to do so. The unequal influences of the changing conditions of life were minimised to some extent by the adoption of uniform methods of housing, feeding, and exercise, which involved the keeping of each individual hen in a single house and run, and entailed the use of extensive plant and labour (see fig. 165). In this respect, however, notwithstanding the care exercised, it must be admitted that the ideal conditions of uniformity were seldom, if ever, realised; and it is possible that certain exceptions met with in the experiments, otherwise inexplicable, may be due to these obscure conditions.

Importance of Genetics. One fact, however, clearly emerges from the experiments, and that is, that a hen which is not carrying the genetic factors for high egg-production does not produce many eggs, *even under the most favourable conditions*, and in this sense it may be claimed that the genetic factors are of primary importance to egg-production.

Continuous Variation. Another difficulty met with in ascertaining the genetic factors of egg-production, was the continuous nature of the characters investigated. Egg-production is usually measured and expressed by the number of eggs produced in a given time.

New System of Grading Egg-production. In order to analyse the complex and continuous data of egg-production, it was found necessary to formulate a definite system of uniform gradings. This method was adopted from 1911 for egg-size and egg-colour (Hurst, 1913) (p. 462), though it was not adopted until later for egg-number. The alternative

system of analysing the data by the use of Means or Averages was tried, only to be rejected. Apart from the considerable labour involved in the computations of the averages, it was found that this method only served to obscure the realities. The mode, however, was used, and proved to be indispensable as a means of expressing the egg-size and egg-colour peculiar to an individual hen. The adoption of a system of uniform percentage gradings to express the rate of egg-production of each individual hen, in place of the methods hitherto used of grading layers by their annual or winter numerical records of production, led eventually to the identification of the genetic factors concerned in egg-production.

Old Methods of Grading. The numerical gradings generally used by poultry breeders proved to be inadequate and inaccurate as a measure of production in White Leghorns and White Wyandottes. The winter records particularly proved to be misleading, for it was evident that they depended to a great extent on external conditions, the most important influence being the date of hatching.

The annual records, depending largely on the winter records, were similarly affected, though on the whole they gave a more accurate measure of egg-production than the winter records. In the alternative system adopted, the unit of time for egg-production is taken as 100 days, with a 50 days' minimum, and the rate of production for the winter period, or for other periods, is calculated and expressed in percentages. These percentages are uniformly graded in tens.

Genetic Factors Identified. As the work proceeded, it was evident that more than one genetic factor was concerned in the annual egg-production of White Leghorns and White Wyandottes. Eventually, seven main factors were identified, five of which influence the number of eggs produced; and of these, two determine winter production, one spring production, one autumn production, while the fifth may affect all three periods of production. The two remaining factors influence the size and colour of the eggs. In addition to the above main factors, there are indications in the data of the presence of several secondary sub-factors, which influence egg-production, but the numbers are too small to work out their genetics satisfactorily.

Material Used. In the course of the experiments 430 pullets of four generations were reared from mated pairs, each pullet was housed and penned singly, and tested for egg-production for a period of one year after her first egg, where possible¹.

¹ These numbers include the progeny of birds of other breeds used for testing the Leghorns and Wyandottes. (*Note added 1924.*)

The factorial constitutions of 42 sires and 135 dams for the seven genetic factors for egg-production were determined as far as possible¹.

Breeds. One light and one heavy breed were chosen for the experiments, namely, White Leghorn and White Wyandötte.

Strains. Three different strains of each breed were used. First, a local strain that had been selected for egg-production for 15 years, on the lines of pen records and mass selection. The White Leghorns of this strain were those used in my previous experiments in 1901—1905, to investigate the genetics of down colour and comb form (Hurst, 1905 and 1907). (See p. 214.)

Second, strains from the West of England, pedigreed for two generations from high producers on both sides.

Third, strains from Lancashire, pedigreed for three generations from high producers on both sides.

Records. In the course of the experiment more than 50,000 eggs were recorded, and each egg was weighed and graded for size and colour.

(2) HISTORY OF GENETIC EXPERIMENTS IN EGG-PRODUCTION.

PEARL'S EXPERIMENTS WITH PLYMOUTH ROCKS.

In 1912 a new light was thrown on the problem of egg-production by Pearl, to whom we owe the first discovery of genetic factors for winter egg-production based on data obtained in his experiments of 1908—1911 with Plymouth Rocks (Pearl, 1912). In addition to the basic genetic factor for femaleness common to all pullets that lay eggs, Pearl found two other genetic factors L_1 and L_2 , which, being present together, determine a high winter production of *over* 30 eggs. The presence of either factor alone gives a low winter production of *under* 30 eggs, while the absence of both factors gives a Zero bird, which fails to produce eggs at all in the winter.

Further, an interesting and important complication observed by Pearl in Plymouth Rocks was, that while the factor L_1 follows simple Mendelian rules, the factor L_2 is sex-linked. That is to say, when the gametes of the Plymouth Rock hen are formed, the factor L_2 is always coupled or linked with maleness, and is never associated with femaleness. Consequently, the high producing Plymouth Rock hen does not transmit her high-production factor L_2 to any of her daughters, but only to her

¹ These numbers include the sires and dams used of breeds other than White Leghorns and White Wyandottes. (*Note added 1924.*)

sons, and therefore the high-producing Plymouth Rock pullet inherits the high-production factor L_2 from her sire and not from her dam.

BURBAGE EXPERIMENTS WITH WHITE LEGHORNS
AND WHITE WYANDOTTES.

From 1913—1916, the Burbage experiments were continued in the light of Pearl's discoveries, but unfortunately they had to be abandoned in April, 1916, owing to the absence of the author on military service from August, 1914, and the similar absence of his recorder, Mr J. B. Perkins, from April, 1916. The six years' records from 1910—1916, however, provide sufficient data to identify the main genetic factors concerned in the first year's production of White Leghorns and White Wyandottes.

Pearl's discovery of the presence of two genetic factors which determine winter production in Plymouth Rocks is clearly confirmed in both White Leghorns and White Wyandottes, with two important modifications. First: No sex-linkage was found, either in the White Leghorns or the White Wyandottes used in the experiments, the hens handing on both the winter production factors to their daughters as well as to their sons. Second: Pearl's interpretation that the Zero winter producers in Plymouth Rocks are mostly due to the absence of both production factors is not borne out in the White Leghorns or the White Wyandottes used in the experiments. For no Zero winter producers appeared in the White Leghorns, and the double recessives gave a low winter production in both breeds, while all the Zeros tested were carrying one of the factors for high winter production.

GOODALE'S EXPERIMENTS WITH RHODE ISLAND REDS.

In 1918 a second landmark in the literature of the subject appeared, which is second only in importance to Pearl's report of 1912. This is Goodale's survey of the general problem of egg-production in Rhode Island Reds, based on four years' experiments with that breed (Goodale, 1918). Goodale's survey corresponds closely with my own experience with White Wyandottes (with a few exceptions of minor importance), and clearly indicates the line of attack necessary for the solution of the problem.

In 1919, Goodale and MacMullen published five years' data of Rhode Island Reds, 1913—1917, and presented an alternative theory for winter production in Rhode Island Reds, to that of Pearl in Plymouth Rocks, in which the factors A and B replace Pearl's factors L_1 and L_2 ,

and there is no Sex-linkage (Goodale, 1919). At the same time, Goodale expresses the belief that the methods used by both Pearl and himself are inadequate to solve the problem, and finally concludes that the mode of inheritance of winter egg-production remains to be determined, and that the problem should be approached from an entirely different angle, namely, that of the inheritance of the several factors whose combined action results in a given number of eggs (cf. Goodale, 1918).

With this I agree, and submit that the results now presented provide a preliminary solution, at all events, of the main problem of the genetics of egg-production. It is to be regretted that the outbreak of war prevented the continuation and completion of the investigation, but it is hoped that the report may serve a useful purpose as a foundation for future work in the identification of other genetic factors and sub-factors of egg-production, whose presence and influence are indicated in the data presented.

GENETIC FACTORS OF EGG-PRODUCTION IN WHITE LEGHORNS AND WHITE WYANDOTTES.

The seven pairs of Mendelian factors identified with the first year's egg-production of three strains of Utility White Leghorn and White Wyandotte hens are as follows:

E (Early)	e (Late)	Sexual maturity
W (Fast)	w (Slow)	Rate of winter production
S (Fast)	s (Slow)	Rate of spring production
M (Slow)	m (Fast)	Rate of autumn production
H (Broody)	m (Non-broody)	Instinct
N (Small)	n (Large)	Egg-mode
C (Brown)	c (White)	Egg-mode

(3) SEXUAL MATURITY (E FACTOR).

The genetic factor E represents Early Sexual Maturity in pullets and is alternative to e which represents Late Sexual Maturity. Early (E) is dominant and Late (e) recessive. Sexual Maturity (S.M.) is measured by the age of the pullet at first egg, which, in the White Leghorns and White Wyandottes used, ranged from 134 to 401 days. S.M. is graded uniformly into months of 30 days, giving a range of ten grades from 4 to 13 inclusive.

The results show that the genetic division line between Early (E) and Late (e) lies at or about 270 days, *i.e.*, between grades 8 and 9. The Early grades (E) are, therefore, from 4 to 8 inclusive, while the Late

grades (e) are from 9 to 13 inclusive. So that somatically, each individual pullet can be graded, described and classified as E 4—E 5—E 6—E 7—E 8 (Early), and e 9—e 10—e 11—e 12—e 13 (Late), while genetically, the formula will be extended to EE 4...Ee 8 and ee 9...ee 13 for the hens, and EE—Ee—ee for the cocks. This system of classification is equally applicable to each of the seven genetic factors for egg-production, and in the extended form serves to show at a glance not only what a hen is, but what she will breed, and in the case of a cock what he will throw.

Owing to the difficulty of expressing orally the Mendelian factor-pairs in terms of the customary capital and small-letter symbols, it may be useful to call EE Double-Early, Ee Single-Early, ee Double-Late, and so on with each of the seven factors of egg-production, the significance of which is obvious.

Table I gives a summary of the various matings made, arranged according to the factorial constitutions of the sires and dams used, with the E and e grades of their daughters. The tables are arranged in three sections: (a) Daughters sired by White Leghorns; (b) Daughters sired by White Wyandottes, and (c) Daughters sired by both breeds.

Throughout the experiments the factorial constitutions of the sires and dams were ascertained and tested in four different ways, namely:

(1) *The Somatic or external Test*, applicable to the dams only, e.g., if the dam was a Late Maturer (e) she was classed as ee. If she was an Early Maturer (E) she was either EE or Ee, and was tested by the:

(2) *Progeny Qualitative Test*, and her factorial constitution determined qualitatively by the E or e grades of her daughters, she was further tested by the:

(3) *Parental Test*, in which her factorial constitution was compared with, and checked by that of her parents, and, where possible, she was finally tested by the:

(4) *Progeny Quantitative Test*, and her factorial constitution tested quantitatively by the ratios of her daughters (E:e).

A factorial constitution that agreed with the four tests was accepted as correct, and an agreement between any two or three of the tests was also accepted in the event of the other tests not being possible, but not otherwise.

The sires were tested by Tests (2), (3), and (4), where possible. In many cases the numbers in a single family were too small to rely on Test (4), which is the ordinary Mendelian F_2 Ratio Test used in other experiments with large numbers as the primary test of genetic consti-

TABLE I. E FACTOR. SEXUAL MATURITY (Age at First Egg).

(a) *Daughters Sired by White Leghorns.*

Matings			Offspring			S.M. Grades (months of 30 days)											Observed		Calculated	
Sires			Dams		Daughters	Early						Late					Early		Late	
Nos.	Factors	Nos.	Factors	Nos.		4	5	6	7	8	9	10	11	12	13	Early	Late	Early	Late	
7	EE	9	EE	42		—	5	21	14	2	—	—	—	—	—	42	0	42.00	0.00	
7	EE	32	Ee	74		—	3	29	19	21	2	—	—	—	—	72	2	74.00	0.00	
1	Ee	1	EE	6		—	3	3	—	—	—	—	—	—	—	6	0	6.00	0.00	
2	EE	2	ee	9		—	—	1	2	6	—	—	—	—	—	9	0	9.00	0.00	
2	Ee	2	Ee	19		—	—	6	7	3	2	—	—	1	—	16	3	14.25	4.75	
19	—	46	—	150		—	11	60	42	32	4	—	—	1	—	145	5	145.25	4.75	

(b) *Daughters Sired by White Wyandottes.*

Nos.	Factors	Nos.	Factors	Nos.	Daughters	1	7	2	6	3	—	—	—	—	—	—	—	—	—
2	EE	2	EE	19		—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	EE	3	Ee	30		—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	Ee	2	EE	12		—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	EE	1	ee	14		—	—	—	—	—	—	—	—	—	—	—	—	—	—
4	Ee	19	Ee	63		—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	Ee	7	ee	28		—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	ee	4	Ee	15		—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	ee	1	ee	4		—	—	—	—	—	—	—	—	—	—	—	—	—	—
14	—	39	—	185		—	—	—	—	—	—	—	—	—	—	—	—	—	—
						1	7	30	60	43	22	18	3	—	1	141	44	143.75	41.25

(c) *Daughters Sired by White Leghorns and White Wyandottes.*

Matings			Offspring		S.M. Grades (months of 30 days)										Observed		Calculated	
Sires		Dams		Daughters	Early					Late					Early	Late	Early	Late
Nos.	Factors	Nos.	Factors	Nos.	4	5	6	7	8	9	10	11	12	13	Early	Late	Early	Late
9	EE	11	EE	61	1	12	23	20	5	—	—	—	—	—	61	0	61·00	0·00
9	EE	35	Ee	104	—	3	39	35	24	3	—	—	—	—	101	3	104·00	0·00
2	Ee	3	EE	18	—	3	7	8	—	—	—	—	—	—	18	0	18·00	0·00
3	EE	3	ee	23	—	—	4	11	8	—	—	—	—	—	23	0	23·00	0·00
6	Ee	21	Ee	82	—	—	16	19	25	13	5	3	1	—	60	22	61·50	20·50
1	Ee	7	ee	28	—	—	1	7	5	6	9	—	—	—	13	15	14·00	14·00
2	ee	4	Ee	15	—	—	—	2	7	3	3	—	—	—	9	6	7·50	7·50
1	ee	1	ee	4	—	—	—	—	1	1	1	—	—	1	1	3	0·00	4·00
33	—	85	—	335	1	18	90	102	75	26	18	3	1	1	286	49	289·00	46·00

Mendelian expectations: A—all Early; B—3 Early: 1 Late; C—1 Early: 1 Late; D—all Late.

tution. This test, however, is not altogether a satisfactory one for the comparatively small families of females reared to maturity in experiments with Poultry, as pointed out by Goodale (1919), though in his experiments and those of Pearl (1912), their difficulties were increased by reason of the two-character ratios concerned. As a matter of fact in the present experiments Test (4), though used, was seldom or very rarely relied on as a Test, and, strictly speaking, might have been dispensed with altogether, as Tests (1), (2) and (3) were usually sufficient and satisfactory. The facility with which the factorial constitutions of 42 sires and 135 dams of various breeds were determined and harmonised by these tests, sufficiently indicates the soundness of the scheme adopted, apart from the general fitness of the Mendelian Ratios shown in the summarised Tables for Leghorns and Wyandottes.

It may be mentioned that in the 2nd and 3rd generations the birds were closely inbred, and matings of sire with daughter and dam with son were frequent.

Table I shows that out of 335 daughters, graded for Sexual Maturity, there are 286 Early and 49 Late, while the Mendelian Expectation, from the matings made, is 289 Early and 46 Late.

An analysis of Table I shows the presence of 4 definite exceptions, 2 White Leghorns and 2 White Wyandottes, as follows:

(1) L 114 [IL ♀ (Ee) × L 13 ♂ (EE)]. Hatched April 3rd, 1912; first egg January 3rd, 1913; S.M. 275 days (grade 9), *i.e.*, 6 days *later* than expected.

(2) L 568 [L 119 ♀ (Ee 8) × L 500 ♂ (EE)]. Hatched May 15th, 1913; first egg February 13th, 1914; S.M. 274 days (grade 9); *i.e.*, 5 days *later* than expected.

(3) W 665 [(W 89 ♀ (Ee 6) × WP 4 ♂ (EE)]. Hatched April 11th, 1915; first egg January 11th, 1916; S.M. 275 days (grade 9), *i.e.*, 6 days *later* than expected.

(4) WL 635 [WL 378 ♀ (ee 10 Z) × W 575 ♂ (ee)]. Hatched March 26th, 1914; first egg December 16th, 1914; S.M. 265 days (grade 8), *i.e.*, 5 days *earlier* than expected.

Of the above only L 568 was bred from, and though a Somatic "Late," proved to be a genetic Early (Ee), and as the margins in each case are only a few days, it seems probable that the other three exceptions are in the same category. In view of the influence of external conditions on Maturity, such cases are not unexpected.

The fact that the Leghorns on the whole matured about a month earlier than the Wyandottes may be due to the larger proportion of EE

parents in the Leghorns, rather than to any intrinsic difference in the two breeds.

There are indications in Table I that the dominance of Early over Late is incomplete, and that the untrue breeder tends to be intermediate. This suggests the possibility of distinguishing some of the true breeders from the untrue breeders without a breeding test by the selection of the Earlier grades. At the same time it is evident that owing to overlapping the method would necessarily involve some uncertainty and the only sure method is the Parental or Progeny test.

There are also indications of the presence of an earlier sub-factor E^1 in the Leghorns with a S.M. of under 240 days (grades 5—7), but the numbers are insufficient to determine this point.

Finally with regard to the nature of the E and e factors, and their influence in hastening or delaying Sexual Maturity, nothing definite has been made out. Goodale (1918) in his survey of egg-production, assumes three pairs of hypothetical growth factors, namely:

- (1) Rapid and Slow Rate of Growth.
- (2) Short and Long Growing Period.
- (3) Early and Late Sexual Maturity.

In these experiments no definite observations were made concerning (1) and (2), so that only data of (3) are available. We have already seen that (3) presents a single factorial difference represented by the factors E and e.

(4) RATE OF WINTER PRODUCTION (W FACTOR).

The genetic factor W represents a Fast or more continuous rate of winter production in pullets, and is alternative to w, which represents a slow or more discontinuous rate of production. Fast (W) is dominant and Slow (w) is recessive.

The rate of winter production (R.W.P.) is measured by the percentage of eggs laid to the number of days from the first egg to the last day of February, and only records of 50 days and over are included.

GRADES.

In these experiments R.W.P. ranges from 83.6 per cent. to 14.7 per cent. Graded in tens there are eight grades of percentages, ranging from 8 to 1. The results show that the genetic division line between Fast (W) and Slow (w) lies at or about 30 per cent., *i.e.*, between grades 2 and 3. The Fast (W) grades are 8 to 3 inclusive, and the Slow (w) are 2 and 1.

TABLE II. W FACTOR. RATE OF WINTER PRODUCTION (from First Egg to March 1st).
(a) *Daughters Sired by White Leghorns.*

Matings				Offspring		R.W.P. Grades (percentages in tens)										Observed		Calculated	
Sires		Dams		Daughters	Nos.	Fast								Slow		Zero	Fast	Slow	
Nos.	Factors	Nos.	Factors			8	7	6	5	4	3	2	1	Nil					
3	WW	3	WW		15	—	1	3	6	1	4	—	—	—	15	0	15·00	0·00	
4	WW	4	Ww		32	—	1	6	13	9	2	—	—	—	31	0	31·00	0·00	
1	Ww	1	WW		3	—	—	—	—	2	1	—	—	—	3	0	3·00	0·00	
2	WW	3	ww		15	—	—	—	3	5	2	4	—	—	15	0	15·00	0·00	
3	WW	16	Ww		34	—	—	2	5	7	10	8	—	—	24	10	25·50	8·50	
1	Ww	1	ww		1	—	—	—	1	—	—	—	—	—	1	0	0·50	0·50	
3	ww	14	Ww		28	—	—	—	1	—	6	8	11	—	15	13	14·00	14·00	
2	ww	2	ww		7	—	—	—	—	—	—	1	4	—	1	6	0·00	7·00	
19	—	44	—		135	—	2	14	31	28	30	23	6	1	105	29	104·00	30·00	

(b) *Daughters Sired by White Wyandottes.*

4	WW	7	WW	WW	64	—	4	14	20	16	7	1	—	2	61	62·00	0·00
4	WW	4	Ww	Ww	22	—	—	2	7	5	7	—	—	1	21	21·00	0·00
2	Ww	6	WW	WW	11	—	—	1	6	2	2	—	—	0	11	11·00	0·00
4	Ww	16	Ww	Ww	20	—	1	1	4	5	1	5	—	3	12	12·75	4·25
2	WW	3	Zero	Zero	22	—	4	14	1	1	—	—	—	1	21	21·00	0·00
1	Ww	1	Zero	Zero	2	—	—	1	—	—	—	—	—	—	—	—	—
17	—	37	—	—	141	1	9	33	38	29	17	6	—	6	127·75	4·25	—

(c) *Daughters Sired by White Leghorns and White Wyandottes.*

Matings			Offspring		R. W. P. Grades (percentages in tens)										Observed		Calculated	
Sires		Dams		Daughters	Fast								Slow	Zero	Fast	Slow	Fast	Slow
Nos.	Factors	Nos.	Factors	Nos.	8	7	6	5	4	3	2	1	Nil	2	76	1	77.00	0.00
7	WW	10	WW	79	—	5	17	26	17	11	1	—	2	—	52	0	52.00	0.00
8	WW	8	Ww	54	—	1	8	20	14	9	—	—	2	—	14	0	14.00	0.00
3	Ww	7	WW	14	—	—	1	6	4	3	—	—	—	—	15	0	15.00	0.00
2	WW	3	ww	15	—	—	3	5	3	4	—	—	—	—	—	—	—	—
7	Ww	32	Ww	54	—	1	3	9	12	11	13	2	2	3	36	15	38.25	12.75
1	Ww	1	ww	1	—	—	—	1	—	—	—	—	—	—	1	0	0.50	0.50
3	ww	14	Ww	28	—	—	—	1	6	8	11	2	—	—	15	13	14.00	14.00
2	ww	2	ww	7	—	—	—	—	—	1	4	2	—	—	1	6	0.00	7.00
2	WW	3	Zero	22	1	4	14	1	1	—	—	—	—	—	21	0	21.00	0.00
1	Ww	1	Zero	2	—	—	1	—	—	—	—	—	1	—	—	—	—	—
36	—	81		276 ¹	1	11	47	69	57	47	29	6	9	6	231	35	231.75	34.25

Mendelian expectations: A—all Fast; B: 3 Fast: 1 Slow; C—1 Fast: 1 Slow; D—all Slow.

¹ Including 9 "Zeros" and 1 "Fast" bred from a "Zero" dam omitted from the calculation.

Externally each pullet is graded as W 8...W 3 (Fast), and w 2, w 1 (Slow). Genetically this is extended to WW 8 (Double-Fast)...Ww 3 (Single-Fast) and ww 2, ww 1 (Double-Slow) for the hens, while the cocks are WW (Double-Fast), Ww (Single-Fast), and ww (Double-Slow).

Table II gives a summary of the results of the various matings. Out of 266 daughters there are 231 Fast (W) and 35 Slow (w), the Mendelian Calculation being 231.75 Fast (W), and 34.25 Slow (w).

EXCEPTIONS.

Two definite exceptions appeared, 1 Leghorn and 1 Wyandotte, namely: (1) L 264 [L 213 ♀ (ww) × L 580 ♂ (ww)] produced 19 eggs in 50 days, or 38 per cent. (W 3 grade), *i.e.*, 8.1 per cent. *over* the Slow Standard expected: (2) W 99 [W 1 ♀ (WW 7) × W 6 ♂ (WW)] produced 31 eggs in 124 days, or 25.0 per cent. (w 2 grade), *i.e.*, 5 per cent. *under* the Fast Standard expected.

It will be observed that the Leghorn exception was only tested for 50 days, which is the minimum period for classification, and 5 sisters were (w) as expected. The Wyandotte exception died a month after completing the test, and was probably unhealthy, while 13 sisters were (W) as expected. The fact that on the whole the Wyandottes laid faster in the winter than the Leghorns may be due to the larger proportion of WW parents in the Wyandottes.

There are indications in the data of the presence of a sub-factor W¹ in the Wyandottes, with a faster R.W.P. of over 45 per cent. (grades 8 to 4½), but the numbers are insufficient to demonstrate this satisfactorily.

Following Pearl and Goodale, the period of winter production is taken as from first egg to the last day of February. The reasons for this have been discussed at length by both authors, and are fully confirmed by my data.

The adoption of a percentage system of grading winter production avoids many of the difficulties arising out of the variable winter cycles of individual birds.

For practical convenience, when breeding from pullets, the end of the winter period may be taken as the last day of January, instead of February, which, on the percentage system, gives equivalent results.

WINTER ZEROS (Laying no Winter Eggs).

Nine of Pearl's winter zero birds appeared in the White Wyandottes and Wyandotte-Leghorns. All were Late-Maturers (ee), ranging from ee 10 to ee 13, and consequently could not lay before March 1st, from their dates of hatching.

If these Zero birds had been hatched a month or two earlier they would, no doubt, have laid a few eggs before March 1st, and would not have been classed as Zeros. In a few cases they might have been tested for W for the 50 days by being hatched in January.

Fortunately, we are not dependent on the External Test for W; we can put them to the Parental Test (see p. 475), which in five cases out of nine shows them to be carrying W. The remaining four cannot be tested by any available test, owing to the fact that at the time the experiments were made the significance of this point was not understood, or *ad hoc* experiments would have been made by the use of the progeny test and early hatches.

The details of the five tested Zero birds are as follows:

(1) W 399 [W 1 ♀ (Ee 7 . WW 7) × W 6 ♂ (Ee . WW)].
Hatched May 13th, 1912; first egg March 11th, 1913; S.M. 302 days (Grade 10); R.W.P. Zero (ee 10 . WW).

(2) W 370 [W 3 ♀ (Ee 7 . WW 4) × W 7 ♂ (Ee . WW)].
Hatched May 6th, 1912; first egg March 11th, 1913; S.M. 309 days (Grade 10); R.W.P. Zero (ee 10 . WW).

(3) W 723 [W 535 ♀ (ee 10 . Zero) × W 554 ♂ (Ee . WW)].
Hatched April 15th, 1915; first egg March 5th, 1916; S.M. 325 days (Grade 10); R.W.P. Zero (ee 10 . W).

(4) W 245 [W 2 ♀ (Ee 7 . Ww 4) × W 7 ♂ (Ee . WW)].
Hatched April 20th, 1912; first egg March 19th, 1913; S.M. 333 days (Grade 11); R.W.P. Zero (ee 11 . W).

(5) WL 600 [W 22 ♀ (Ee 8 . Ww 4) × L 588 ♂ (Ee . WW)].
Hatched March 27th, 1914; first egg March 23rd, 1915; S.M. 361 days (Grade 12); R.W.P. Zero (ee 12 . W).

It is evident that a normal winter Zero Wyandotte, hatched at a normal time, is simply a *Very Late Maturer* (ee). We have seen that a Wyandotte Zero (ee) may carry the factor W, which cannot be expressed unless the bird be hatched *abnormally early*. From this it would appear that the Zero Wyandotte differs in degree only from the birds that lay a few eggs before March 1st, and in this sense may be regarded as a somatic rather than a genetic Zero.

Goodale apparently comes to the same conclusion concerning the Rhode Island Red Zeros, and regards them as a purely artificial class. In some cases he omits them from the records (1918), while in others he groups them with the Mediocre-Producers (1919).

On the other hand, Pearl (1912), while admitting that some of the Plymouth Rock Zeros are pathological giving a somatic Zero record,

regards genetic Zeros as due to the double absence of the two production factors L_1 and L_2 , making their factorial constitution $l_1 l_2$, which is apparently equivalent to (ew) in our Wyandottes and Leghorns. Only one Leghorn (ew) and one Wyandotte (ew) could be tested in the experiments, and both laid a few eggs before March 1st. It is, however, possible that the Zero Wyandotte may be due to a sub-factor e^a , which determines extreme lateness of maturity, and in that case would be genetic.

Further experiments with Zeros are required to determine this point.

(5) RATE OF SPRING PRODUCTION (S FACTOR).

The genetic factor S represents a Fast or more continuous rate of spring and early summer production by a hen in her first season's laying, and is alternative to s, which represents a Slow or more discontinuous rate of spring production. Fast (S) is dominant, and Slow (s) is recessive.

The rate of spring production (R.S.P.) is measured by the percentage of eggs laid in the 122 days between March 1st and June 30th inclusive.

In these experiments R.S.P. ranged from 89.3 per cent. to 18.1 per cent. Graded into tens there are eight grades, ranging from 8 to 1.

As in R.W.P., the genetic division line between Fast (S) and Slow (s) lies at or about 30 per cent., *i.e.*, between grades 2 and 3. Consequently the Fast (S) grades are 8 to 3 inclusive, and the Slow (s) grades are 2 and 1.

Externally each hen is graded as S 8...S 3 (Fast) and s 2, s 1 (Slow). Genetically this is extended to SS 8 (Double-Fast)...Ss 3 (Single-Fast), and ss 2, ss 1 (Double-Slow) for the hens, while the cocks are SS (Double-Fast), Ss (Single-Fast) and ss (Double-Slow).

Table III gives a summary of the results of the various matings. Out of 224 daughters there are 216 Fast (S) and 8 Slow (s), the Mendelian Calculation being 217.25 Fast (S) and 6.75 Slow (s).

Exceptions. One definite exception appeared namely:—WL 92 [L 21 ♀ (SS 6) × W 10 ♂ (SS)], which laid 29 eggs in the 122 days, or 23.7 per cent., *i.e.*, 6.3 per cent. *slower* than expected. This bird moulted deeply in May, and laid no more eggs during the year. Her first year's production was only 69, notwithstanding a winter production of 40. The fact that her 17 sisters were all Fast spring producers, ranging from 43.4 per cent. to 69.6 per cent., suggests that she was abnormal in some way.

The fact that on the whole the Leghorns laid faster in the spring

TABLE III. S FACTOR. RATE OF SPRING PRODUCTION (March 1st to June 30th).
(a) *Daughters Sired by White Leghorns.*

Matings				Offspring		R.S.P. Grades (percentages in tens)										Observed		Calculated	
Sires		Dams		Daughters				Fast					Slow						
Nos.	Factors	Nos.	Factors	Nos.		8	7	6	5	4	3	2	1	Fast	Slow	Fast	Slow		
7	SS	13	SS	68	—	17	30	14	7	—	—	—	—	68	0	68·00	0·00		
1	SS	3	Ss	4	—	—	—	—	1	2	1	—	—	4	0	4·00	0·00		
2	Ss	20	SS	24	—	3	8	9	3	1	—	—	—	24	0	24·00	0·00		
1	SS	1	ss	1	—	1	—	—	—	—	—	—	—	1	0	1·00	0·00		
1	Ss	1	Ss	1	—	—	—	—	—	—	—	1	—	0	1	0·75	0·25		
12	—	38	—	98	—	21	38	24	12	2	1	1	—	97	1	97·75	0·25		

(b) *Daughters Sired by White Wyandottes.*

4	SS	5	SS	34	1	2	15	14	1	—	1	—	33	1	34·00	0·00
2	SS	2	Ss	25	—	2	15	1	2	2	—	—	25	0	25·00	0·00
3	Ss	16	SS	41	—	6	13	14	8	—	—	—	41	0	41·00	0·00
4	Ss	8	Ss	26	—	1	4	7	6	2	2	4	20	6	19·50	6·50
13	—	31	—	126	1	11	47	39	17	4	3	4	119	7	119·50	6·50

(c) *Daughters Sired by White Leghorns and White Wyandottes.*

11	SS	18	SS	102	1	19	45	28	8	—	1	—	101	1	102·00	0·00
3	SS	5	Ss	29	—	2	15	5	4	3	—	—	29	0	29·00	0·00
5	Ss	36	SS	65	—	9	21	23	11	1	—	—	65	0	65·00	0·00
1	SS	1	ss	1	—	1	—	—	—	—	—	—	1	0	1·00	0·00
5	Ss	9	Ss	27	—	1	4	7	6	2	3	4	20	7	20·25	6·75
25	—	69	—	224	1	32	85	63	29	6	4	4	216	8	217·25	6·75

Mendelian expectations: A—all Fast; B—3 Fast; 1 Slow.

than the Wyandottes, may be due to the larger proportion of SS parents in the Leghorns.

The precise nature of the difference between Fast (S) and Slow (s) birds in R.S.P. has not been made out, but there are several indications in the data that it is of a pathological nature, or possibly a lack of vigour and stamina, which may or may not be pathological.

In any case, there appears to be a definite difference between the nature of the Fast (S) birds and the Fast (W) birds, and especially between the Slow (s) birds and the Slow (w) birds, in spite of their being measured on a common basis of Rate of Production. Mainly, it may be regarded as a difference of rhythm. Both the Fast (S) and the Fast (W) birds lay at a more or less continuous rate, but the speed of the Fast (S) is distinctly higher and more continuous than the speed of the Fast (W). For instance, the mode rate of W for Leghorns and Wyandottes is grade 5 (with grade 4 prominent), while the mode rate of S for practically the same birds is grade 6. Possibly the higher temperature at this period may influence the Rate of Production. It is, however, in the Slow (S) and the Slow (w) that the difference between R.S.P. and R.W.P. is perceived, for the rhythm is, as a rule, very different. Both are discontinuous, but the discontinuity in the Slow (w) is more regular than that of the Slow (s). As a rule, the Slow (w) birds lay 8—10 eggs, more or less continuously, and then stop for a few weeks, though some continue to lay odd eggs at infrequent intervals. On the other hand, the Slow (s) birds lay 16—20 eggs more or less continuously, and then stop for one or two months, or more, and may or may not fall into moult. It may be that the Slow (s) birds are slow because they lack vigour and stamina, while the Slow (w) are vigorous birds, with a natural discontinuous rhythm.

It may be noted that most of the Slow (w) birds are Fast (S) spring producers, and there seems to be no definite association between the Slow (s) and the Slow (w) factors.

There are indications in the data of the presence of a sub-factor S¹ in the Wyandottes (and possibly in the Leghorns) with a faster R.S.P. of 50 per cent. and over (grades 8—5), but the numbers are insufficient to determine this definitely.

A distinct difference was observed between the strains used in the experiments in regard to the proportion of SS birds.

In the strain based on Mass Selection there were 94·1 per cent. of SS birds, while in the two pedigree strains there were 57·1 per cent. and 54·5 per cent. respectively.

The explanation, probably, is that while the Mass Selection birds were selected primarily for vigour and stamina, the pedigree birds were primarily selected for individual egg-production, with vigour and stamina a secondary consideration, which supports the idea that the factor S may represent vigour and stamina.

(6) RATE OF AUTUMN PRODUCTION (M FACTOR).

The factor M represents a Slow or more discontinuous production in the late summer and autumn at the end of the first year's laying; it is alternative to m, which represents a Fast or more continuous autumn production. Unlike R.W.P. and R.S.P., Slow (M) is in this case dominant, while Fast (m) is recessive.

The rate of autumn production (R.A.P.) is measured by the percentage of eggs laid from July 1st to the end of the laying year, with a minimum of 50 days.

In these experiments R.A.P. ranged from 65·8 per cent. to 1·2 per cent., and there were three autumn Zeros.

Graded in tens, there are seven grades ranging from 0 to 6. As in R.W.P. and R.S.P., the genetic division line between Slow (M) and Fast (m) lies at or about 30 per cent., *i.e.*, between grades 2 and 3.

Table IV gives a summary of the results of the various matings, and out of 197 daughters there were 140 Slow (M) and 54 Fast (m), the Mendelian Calculation being 145·50 Slow (M) and 48·50 Fast (m).

THE EXCEPTIONS.

Two definite exceptions appeared, 1 in the Leghorns and 1 in the Wyandottes, as follows: L 158 [2 L ♀ (MM) × L 14 ♂ (MM)] produced 41 eggs in 121 days of the autumn period, or 33·8 per cent., *i.e.*, 3·9 per cent. *faster* than expected. WL 74 [L 4 ♀ (mm 4) × W 9 ♂ (MM)], produced 39 eggs in 97 days, or 40·2 per cent., *i.e.*, 10·3 per cent. *faster* than expected.

It is possible that the latter exception is due to the incomplete dominance of M, though her 7 sisters did not exhibit it, their R.A.P., ranging from 9·0 per cent. to 26·2 per cent.

The fact that on the whole the Leghorns laid more slowly in the autumn than the Wyandottes may be due to the larger proportion of MM parents in the Leghorns.

TABLE IV. M FACTOR. RATE OF AUTUMN PRODUCTION (July 1st to last egg of year).

(a) Daughters Sired by White Leghorns.

Matings			Offspring		Zero	R.A.P. Grades (percentages in tens)						Observed		Calculated		
Sires	Dams	Daughters	Nos.			Slow		Fast				Slow	Fast	Slow	Fast	
Nos.	Factors	Nos.	Factors	Nos.	Nil	0	1	2	3	4	5	6	Slow	Fast	Slow	Fast
4	MM	27	MM	37	—	11	17	8	1	—	—	—	36	1	37·00	0·00
1	Mm	1	MM	6	—	4	1	1	—	—	—	—	6	0	6·00	0·00
2	MM	4	mm	21	1	8	9	3	—	—	—	—	20	0	20·00	0·00
1	Mm	1	Mm	1	—	—	—	—	1	—	—	—	0	1	0·75	0·25
4	Mm	4	mm	26	—	1	2	5	11	5	1	1	8	18	13·00	13·00
12	—	37	—	91	1	24	29	17	13	5	1	1	70	20	76·75	13·25

(b) Daughters Sired by White Wyandottes.

2	MM	2	Mm	3	—	1	—	—	—	2	—	—	—	—	—	3	0	300	000
1	Mm	2	MM	7	—	4	—	—	—	2	—	—	—	—	—	7	0	700	000
1	MM	2	mm	10	—	2	—	—	—	3	—	—	—	—	—	9	1	1000	000
1	mm	1	MM	2	—	—	—	—	—	1	—	—	—	—	—	2	0	200	000
2	Mm	14	Mm	24	1	4	10	5	4	5	—	—	—	—	19	4	1725	575	
3	Mm	6	mm	45	1	3	8	13	11	9	—	—	—	—	24	20	2200	2200	
2	mm	2	Mm	15	—	—	1	5	3	5	3	1	—	—	6	9	750	750	
12	—	29	—	106	2	14	24	32	18	15	1	—	—	70	34	6875	3525		

(c) *Daughters Sired by White Leghorns and White Wyandottes.*

Matings			Offspring		R.A.P. Grades (percentages in tens)										Observed		Calculated	
Sires		Dams		Daughters		Zero		Slow			Fast			Slow		Fast		
Nos.	Factors	Nos.	Factors	Nos.		Nil		0	1	2	3	4	5	6	Slow	Fast	Fast	
4	MM	27	MM	37				11	17	8	1				36	37.00	0.00	
2	MM	2	Mm	3				1	—	2	—				3	3.00	0.00	
2	MM	3	MM	13		—		8	2	3	—				13	13.00	0.00	
3	Mm	6	mm	31		—		10	12	7	—	1			29	30.00	0.00	
1	Mm	1	MM	2		—		—	1	1	—				2	2.00	0.00	
3	Mm	15	Mm	25		1		4	10	5	5				19	18.00	6.00	
7	Mm	10	mm	71		1		4	10	18	22	14	1	1	32	35.00	35.00	
2	mm	2	Mm	15				—	1	5	3	5	1		6	7.50	7.50	
24	—	66	—	197 ¹		3		38	53	49	31	20	2	1	140	145.50	48.50	

Mendelian Expectation: A—all Slow; B—3 Slow : 1 Fast; C—1 Slow : 1 Fast.

¹ Including 3 zero birds.

NATURE OF THE M FACTOR.

With regard to the nature of the M factor, it is evidently different from the factors W and S, seeing that in the latter Fast Rate is dominant and Slow Rate recessive; while in the M factor the position is reversed, Slow Rate being dominant and Fast recessive. Further, a striking external difference was observed between M and m birds, apparently coinciding with their different rates of production, for, as a rule, the m birds do not fall into a deep moult in the autumn as the M birds do, but undergo a partial moult (by shedding a few feathers from time to time), and keep on laying more or less continuously throughout the autumn, usually for 13 or 14 months after the first egg. It would appear, therefore, that m is a recessive mutation in which the factor M is lost, and the normal deep autumn moult of the M birds is absent. Consequently m birds are partial autumn moulters, while M birds are deep moulters; and m birds are Fast autumn producers while M birds are Slow.

THE MOULT AND EGG PRODUCTION.

On the other hand, it must be admitted that precise data of the relationship between moulting and egg-producing are lacking, and it is not at all clear, *e.g.*, whether egg-production ceases because of the moult, or whether the moult takes place on the cessation of egg-production. All we know is that usually they synchronise.

The recessive m mutation is interesting genetically on account of its comparatively recent appearance, and economically by reason of its having made the "300-egg" record possible in the year.

There are indications in the data that the M birds (deep autumn moulters), when hatched early, are also subject to the winter "neck-moult," and its accompanying cessation of laying, while the m birds (partial autumn moulters) are not, but the numbers are too small to determine this point.

(7) BROODINESS (H FACTOR).

The genetic factor H represents Broodiness, and is alternative to h, which represents Non-Broodiness. Broody (H) is dominant and Non-Broody (h) is recessive. (Hurst 1905 and 1913.) (See pp. 219 and 463.)

The instinct of Broodiness in the hen is very variable in its manifestations in different breeds.

In these experiments the varying degrees or intensity of Broodiness in the White Wyandotte and Wyandotte-Leghorn is measured by the number of times the hen went Broody during the first laying season.

This measure of Broodiness is admittedly imperfect and incomplete in many respects, but it may serve as a temporary measure to cover the limited data dealt with. This gives six grades of Broodiness, and one of Non-Broodiness, grades 6 to 1 being Broody (H) and grade 0 is Non-Broody (h). Owing to the fact that a sensible proportion of Broody hens (about 1 in 6) do not show their Broodiness until their second year of laying, it has not been possible to ascertain the factorial constitution of the "Non-Broodies" in these experiments, as most of them were only observed during their first laying year. The few hens that were observed for a longer period were variable in their manifestations of Broodiness.

For instance, Leghorn L 113 was "Non-Broody" in her first laying season 1912—13, but Broody in her second season, when she was set, and duly hatched and reared chickens.

In another case, Wyandotte W 22 was Broody once in her first season, Non-Broody throughout her second season, and Broody once in her third season. In these circumstances it is obviously difficult to determine a true Non-Broody (hh), and it would require considerable resources to obtain large numbers, seeing that only a small proportion of hens seem to survive more than three or four laying seasons in the highly fecund strains used.

In order to demonstrate the segregation of the Broody factor (H), Table V gives the data of the first laying season of the White Wyandottes and White Leghorns, and for this purpose the Non-Broodies are all tentatively regarded as of factorial constitution (hh).

As expected, on this hypothesis there is an excess of Non-Broodies and a deficiency of Broodies. But if 1 in 6 of the Non-Broodies became Broody in their second season, as they seem to do in the few tested, the numbers observed would be close to the Mendelian expectation.

Thus, taking the Hh \times hh matings, out of 90 daughters there were 33 Broody and 57 Non-Broody.

If 1 in 6 of the 57 Non-Broody became Broody in their second season, the approximate numbers would be 42 Broody and 48 Non-Broody, which is not far from the Mendelian expectation of equality (45 : 45).

On this view the results, in the Wyandottes at all events, are not inconsistent with the hypothesis that Broodiness is due to a single factor (H), though the few Broody exceptions in the Non-Broody Leghorns raise a distinct difficulty in accepting the hypothesis for Broodiness generally.

TABLE V. H FACTOR. BROODINESS.
(a) *Daughters Sired by White Leghorns.*

Matings			Offspring		B. Grades (times Broody first season)						Observed		Calculated		
Sires		Dams	Daughters		Broody						Non-Broody				
Nos.	Factors	Nos.	Factors	Nos.	6	5	4	3	2	1	0	Broody	Non-Broody	Broody	Non-Broody
1	hh	1	Hh	13	—	—	—	—	—	2	11	2	11	6.50	6.50
9	hh	36	hh	78	—	—	—	2	2	—	74	4	74	0.00	78.00
10	—	37	—	91	—	—	—	2	2	2	85	6	85	6.50	84.50

(b) *Daughters Sired by White Wyandottes.*

1	hh	2	HH	6	—	—	1	1	1	3	—	—	6	6.00	0.00
1	Hh	2	Hh	10	—	—	1	1	4	—	4	—	6	7.50	2.50
2	Hh	3	hh	40	—	—	—	3	6	4	24	16	24	20.00	20.00
5	hh	17	Hh	37	—	—	1	6	5	3	22	15	22	18.50	18.50
4	hh	5	hh	17	—	—	—	—	—	1	16	1	16	0.00	17.00
13	—	29	—	110	2	1	3	11	16	11	66	44	66	52.00	58.00

(c) *Daughters Sired by White Leghorns and White Wyandottes.*

(c) <i>Daughters Sired by White Leghorns and White Wyandottes.</i>															
Sires		Dams		Broody						Non-Broody		Broody		Non-Broody	
Nos.	Factors	Nos.	Factors	0	5	4	3	2	1	0	Broody	Non-Broody	Broody	Non-Broody	Calculated
1	hh	2	HH	—	—	—	1	1	1	3	—	—	6	0	0.00
1	Hh	2	Hh	—	—	—	1	1	4	—	—	4	6	4	2.50
2	Hh	3	hh	—	—	—	—	—	—	—	—	—	—	—	—
6	hh	18	Hh	2	1	—	3	6	4	—	24	16	24	24	20.00
				—	—	—	1	6	5	5	33	17	33	33	25.00
13	hh	41	hh	—	—	—	—	2	2	1	90	5	90	90	95.00
23	—	66	—	2	1	3	13	18	13	151	50	151	50	151	142.50

Mendelian Expectation: A—all Broody; B—3 Broody : 1 Non-broody; C 1 Broody : 1 Non-broody; D—all Non-broody.

Since the above scheme was worked out an important contribution has appeared in the *Journal of Genetics* (December, 1920) by Professor Punnett, and the late Major Bailey (whose loss in the War is deeply deplored). This paper gives data of the inheritance of Broodiness in Langshan, Brown Leghorn and Gold-Pencilled Hamburg crosses; and the results resemble those given above for White Wyandottes and White Leghorns, inasmuch as they show a *definite excess of Non-Broodies* in F_2 , which was most marked in the Langshan \times Hamburg cross.

Punnett suggests that the Hamburg may have been carrying a factor which tends to inhibit the development of the Broody habit, but points out that his results are insufficient to decide this point (Punnett and Bailey, 1920).

In view of Punnett's suggestion, I have worked through my results again, and find that, on the whole, they not only support and supplement his evidence, but his hypothesis also seems to bring into line the complicated genetic data of the incidence of Broodiness in the various breeds that have so far been published. It may, therefore, be worth while to present the scheme briefly for consideration.

The appearance of Broodies (H) in the Non-Broody White Leghorns (hh) is a serious difficulty in the way of interpreting Broodiness as due to a single factor (H), and the facts are as follows:—

Out of 84 White Leghorn hens observed during their first laying season, 4 went Broody, namely:—

- (1) L 118 (IL ♀ \times L 13 ♂).
- (2) L 540 (L 5 ♀ \times L 501 ♂).
- (3) L 541 (L 5 ♀ \times L 501 ♂).
- (4) L 515 (L 21 ♀ \times L 501 ♂).

It will be observed that three out of the four are by the same sire, L 501; and L 501 is the son of L 13, who sired the remaining one. So that all the Broody Leghorns trace to L 13 ♂ .

With regard to the dams, L 5 and L 21 were bred from the same pen as L 13, while IL was unrelated to him, so far as is known. At first sight, it might appear that the sires and dams were carrying a complementary recessive factor, which, on meeting its complement, reproduced Broodiness; but this view is not confirmed in the next generation, for no Broodies appeared in the offspring of five sons of L 501 ♂ mated with daughters of L 5 ♀ and her relatives.

Nor could L 13 ♂ and L 501 ♂ be carrying the dominant factor (H) alone (or a second dominant factor H^1), for in that case more than four

Broody daughters would have appeared out of the 34 observed. It would seem, therefore, that the only satisfactory solution of the appearance of these Broodies in the Non-Broody White Leghorns is to postulate the presence of the factor H plus an inhibitory factor, as suggested by Punnett (Punnett and Bailey, 1920).

Expressed in factors: If H is the factor for Broodiness and I its inhibitor, and the sires and dams were of the factorial constitution HhIi, the expected result would be 9 HI : 3 Hi : 3 hI : 1 hi, or 3 Broody : 13 Non-Broody, which is near to the 4 Broody : 17 Non-Broody observed in these Leghorn matings. The scheme also appears to be consistent with the rest of the data. Thus, a second mating (HhIi × hhIi) would give 3 HI : 3 hI : 1 Hi : 1 hi, or 1 Broody to 7 Non-Broody. These identical numbers appeared twice in the data.

A third mating (Hhii × hhIi) would give 1 HI : 1 hI : 1 Hi : 1 hi, or 1 Broody to 3 Non-Broody. The numbers 3 Broody : 9 Non-Broody appeared once in the data. This ratio is interesting as an apparent reversal of the dominance of Broodiness, and may help to explain the phenomena of the reversal of dominance in other characters in animals and plants.

The following matings and their reciprocals also give a ratio of 1 Broody : 3 Non-Broody, with an apparent reversal of dominance:—HHIi × HHii, HHIi × HhIi, HHIi × hhIi, HhIi × hhii. Another mating, HhIi × Hhii, would give 3 HI : 3 Hi : 1 hI : 1 hi, or 3 Broody : 5 Non-Broody. This ratio does not actually appear in the data, and, in any case, would be difficult to distinguish at sight from the ordinary equality ratio, in small numbers. The following matings give the equality ratio of 1 Broody : 1 Non-Broody:—HHIi × HHii, HHIi × Hhii, HHIi × hhii, HhIi × HHii, hhIi × HHii, and Hhii × hhii. Ratios of 4 : 4, 5 : 5, and 8 : 10 appear in the data. Lastly, the mating Hhii × Hhii gives the ordinary ratio of 3 Broody : 1 Non-Broody.

Altogether the HI scheme gives 45 possible matings (without the reciprocals), of which 3 give all Broody, 27 all Non-Broody, 6 give 1 Broody : 1 Non-Broody, 5 give 1 : 3, and 1 mating each gives 1 : 7, 3 : 5, 3 : 13, and 3 Broody : 1 Non-Broody.

Finally, the genetic constitutions of the White Wyandottes in the HI scheme may be HHii, Hhii, or hhii, which is not inconsistent with the original idea that Broodiness in the Wyandotte *appears* to be due to the presence of a single factor (H).

The evidence for the HI scheme is admittedly incomplete, even when Punnett's results are combined with those given above, and experiments

on a considerable scale would be necessary to demonstrate and confirm it. The chief reason for representing it here is that it seems to bring into line most of the complicated and apparently conflicting data on the genetics of Broodiness that have been published. For instance, in 1902 the author found that the intense Broodiness of the Buff Cochin was completely dominant in F_1 to the never-broody strain of Black Hamburgs that had been bred by him at Burbage since 1886. (See p. 219.)

The F_2 of this cross was only observed for juvenile characters, but other experiments in crossing Non-Broody hens together, e.g., White Leghorns, Houdans, and Black Hamburgs, gave all Non-Broody recessives, which, in the early days of Mendelism, was considered sufficient proof of their genetic purity. (Hurst, 1905.) (See p. 217.)

In 1911 Bateson and Punnett found the marked Broodiness of the Silky Fowl equally dominant to the Non-Broody Brown Leghorn, with a *remarkable deficiency of Non-Broodies* in F_2 . (See Bateson and Punnett, 1911.)

In 1912 Punnett and Bailey found the Broody Langshan dominant to both the Non-Broody Brown Leghorn and the Gold-Pencilled Hamburg, with an *excess of Non-Broodies* in F_2 , which was much greater in the Hamburg than in the Leghorn cross (see Punnett and Bailey, 1920). A similar definite *excess of Non-Broodies* has been found in the White Wyandotte and White Leghorn matings noted above. The further fact that the F_1 Cochin-Hamburgs were all (31) intensely Broody like the Cochin, while the F_1 Wyandotte-Leghorns were variable in their degrees of Broodiness, ranging from occasional clucking and ruffling of feathers to close and frequent sitting, is also noteworthy, and apparently inexplicable on a single factor basis.

On the other hand, the HI scheme applied to the above data seems to cover the whole of the results except Bateson and Punnett's Silky-Leghorn cross, which apparently requires the addition of a third dominant factor H^1 , so that the genetic constitution of the Silky Fowl used might be $HH H^1H^1 ii$ and that of the Brown Leghorn $hh h^1h^1 ii$.

The varying degrees of Broodiness manifested in certain cases may be due to the interaction or incomplete dominance of the factor I, for H seems to be completely dominant in the absence of I.

(8) EGG-SIZE (N FACTOR).

The genetic factor N represents the production of Small eggs by hens in their first laying year, and is alternative to n, which represents the production of Large eggs. Small egg (N) is dominant and Large egg (n) is recessive. (Hurst, 1913.) (See p. 462). In these experiments, size of egg is measured by weight, and in the White Leghorns and White Wyandottes used, the weights of individual eggs, with a few exceptions, ranged from 42.5 to 74 grams. These were graded into nine equal grades of 3.5 grams ($\frac{1}{8}$ oz.) each, namely:—

Small Egg-modes (N).	Large Egg-modes (n).
Grade 1 (42.5 and under 46 grams).	Grade 5 (56.5 and under 60 grams).
Grade 2 (46 and under 49.5 grams).	Grade 6 (60 and under 63.5 grams).
Grade 3 (49.5 and under 53 grams).	Grade 7 (63.5 and under 67 grams).
Grade 4 (53 and under 56.5 grams).	Grade 8 (67 and under 70.5 grams).
	Grade 9 (70.5 and under 74 grams).

A few eggs under 42.5 grams ($1\frac{1}{2}$ oz.) were classed with grade 1, and a few eggs over 74 grams ($2\frac{5}{8}$ oz.) were classed with grade 9.

Each egg laid by a hen, during her first year's laying, was weighed and graded, and the *mode-grade of the year* was taken to represent the size of egg laid by each hen.

In most cases the individual hen, during the first year, laid eggs of five to seven different grades, but, with a few exceptions, the mode-grade, *i.e.*, the grade with the largest number of eggs, was definite and distinct from the grades on either side.

As a rule the winter eggs of the pullet, laid before March 1st, were about one grade less in size than those laid after, consequently in cases, where, for one reason or another, only the winter eggs were recorded, the mode-grade was increased by one, in order to place the birds on an equal footing with those that had a full year's mode. It may be mentioned that many methods of representing the size of eggs laid by a hen were tried, but none of these proved so satisfactory as the method finally adopted. (Hurst, 1913.) (See p. 462.)

The results show that the division line between the production of Small-mode (N) and Large-mode (n) eggs lies at or about a mode of 56.5 grams (2 oz.), *i.e.*, between mode-grades 4 and 5. The Small mode-grades (N) are therefore 1 to 4 inclusive, and Large mode-grades (n) are 5 to 9 inclusive.

It is a remarkable coincidence that the genetic division line between N and n proves to be approximately the same as the standard adopted by poultry breeders in their laying competitions¹ (which is higher

¹ In England the standard for First Grade eggs in laying competitions is usually 2 oz. (= approx. 56.7 grams) and over.

than the commercial standard). All I can say is that genetically no other division line will fit the data.

Table VI gives a summary of the various matings, and out of 331 daughters graded for mode-size of egg, there are 135 Small (N) and 196 Large (n) while the Mendelian calculation is 128.75 Small (N) and 202.25 Large (n). Altogether there are 7 definite exceptions, 3 Leghorns and 4 Wyandottes as follows:—

(1) L 516 [L 4 (nn 7) × L 501 (nn)] produced 67 eggs in her first season of mode-grade 4, *i.e.*, one grade *less* than that expected. Her 7 sisters had mode-grades of 5 and 6 (nn), and she was exceptional in other respects; for, in 1914, attempts were made to breed from her, but no chickens from her could be reared, though every egg was set during the hatching season, and she was probably pathological.

(2) L 539 [L 5 ♀ (nn 6) × L 501 ♂ (nn)] produced 144 eggs in her first season of mode-grade 4, *i.e.*, one grade *less* than expected. Her 6 sisters had mode-grades of 5, 6, and 7 (nn) and when mated with L 580 ♂ (nn) she gave 8 daughters, all with mode-grades of 5 or 6 (nn), proving her to be genetically nn.

(3) WL 620 [WL 48 ♀ (nn) × L 579 ♂ (nn)] produced 200 eggs in her first season of mode-grade 3, *i.e.*, two grades *less* than expected. This bird was late hatched (May 22nd, 1914) and was abnormal, inasmuch as her spring and summer mode (3) was one grade less than her winter-mode (4), while her autumn mode was 5, as expected. Her 7 sisters had mode-grades of 5 and 6 (nn).

(4) W 728, W 731 and WP 711 were one grade *less* than expected, but as their year modes were estimated from their winter modes, it is possible that they may not be real exceptions.

(7) W 89 [W 3 ♀ (nn) × W 7 ♂ (NN)] produced 201 eggs in her first season of mode-grade 5, *i.e.*, one grade *larger* than expected. This bird is apparently a real exception for mated to WP 4 ♂ (nn) she produced 6 daughters with mode-grades of 6, 7, and 8 (nn), showing that genetically she was nn, and not Nn as expected from the genetic constitution of her parents. For her dam W 3 was nn, and her sire W 7 was NN, while her 11 sisters were of grades 2, 3 and 4 (N). That her sire was NN is shown by the fact that his 16 other daughters had mode-grades of 2, 3 and 4 (N).

It seems probable that the Wyandotte hen W 89 is a true mutation for Large egg-mode which arose through the sudden and solitary loss of one of the N factors of her sire W 7, which was not repeated in his 15 other offspring observed that season. If this interpretation is correct,

TABLE VI. N FACTOR. EGG-SIZE.

(a) *Daughters Sired by White Leghorns.*

Matings			Offspring		E.S.M. Grades 42.5 to 74 grams in grades of 3.5 grams										Observed		Calculated		
Sires		Dams		Daughters		Small (under 56.5 grams)			Large (56.5 grams and over)							Small		Large	
Nos.	Factors	Nos.	Factors	Nos.	Factors	1	2	3	4	5	6	7	8	9	Small	Large	Small	Large	
1	Nn	9	Nn	9	Nn	—	2	1	3	1	1	1	—	—	6	3	6.75	2.25	
1	Nn	13	nn	17	nn	—	—	2	6	8	—	1	—	—	8	9	8.50	8.50	
2	nn	2	Nn	7	Nn	—	—	1	2	4	—	—	—	—	3	4	3.50	3.50	
8	nn	22	nn	117	nn	—	—	1	2	33	49	16	15	1	3	114	0.00	117.00	
12	—	46	—	150	—	—	2	5	13	46	50	18	15	1	20	130	18.75	131.25	

(b) *Daughters Sired by White Wyandottes.*

Sires		Dams	Daughters										Observed		Calculated		
Nos.	Factors	Nos.	Nos.	Factors	1	2	3	4	5	6	7	8	9	Small	Large	Small	Large
2	NN	2	22	Nn	—	12	5	5	—	—	—	—	—	22	0	22.00	0.00
4	NN	5	50	nn	—	8	21	20	1	—	—	—	—	49	1	50.00	0.00
1	nn	12	17	NN	—	1	6	10	—	—	—	—	—	17	0	17.00	0.00
2	Nn	3	13	nn	—	—	2	6	3	—	—	—	—	8	5	6.50	6.50
3	nn	9	29	Nn	—	—	4	12	11	2	—	—	—	16	13	14.50	14.50
3	nn	8	50	nn	—	—	—	3	12	21	6	8	—	3	47	0.00	50.00
15	—	39	181	—	—	21	38	56	27	25	6	8	—	115	66	110.00	71.00

we here get a glimpse of the manner in which the Large egg character may have come into existence from the small egg of the wild species. In the original case, however, at least two generations would elapse after the germinal change before it appeared as a somatic character, owing to its recessive nature, and the lack of a recessive mate.

The fact that the Leghorns as a whole laid larger eggs than the Wyandotte may be due to the absence of NN parents and the larger proportion of nn parents in the Leghorns.

(9) EGG-COLOUR (C FACTOR).

The genetic factor C represents the production of Brown-shelled eggs, and is alternative to c, which represents the production of White-shelled eggs. Brown (C) is dominant and White (c) is recessive (Hurst 1905 and 1913). (See pp. 219 and 263.) In these experiments egg-colour is graded in 6 colour shades of equal differences of intensity, numbered from 5 to 0.

Grade 5 is Dark-Brown, the deepest shade found in fowls, which in my experience is rather rare in White Wyandottes and Light Sussex, but more common in Rhode Island Reds and Langshans. (Rhode mode.)

Grade 4 is the ordinary Brown egg common in many breeds. (Cochin mode.)

Grade 3 is a Light Brown egg which might be called the mode-colour of White Wyandottes and Light Sussex. (Wyandotte mode.)

Grade 2 is a Cream-tinted White egg, which is the mode-colour of the Old English Pit-Game. This colour is also produced by White Wyandottes, Light Sussex, and more rarely by White Leghorns. (Game mode.)

Grade 1 is an Ivory-Tinted White egg which is the mode-colour of White Leghorns, and rarely produced by the Pit-Game and the White Wyandotte. (Leghorn mode.)

Grade 0 is a clear Chalky White produced only by certain White Leghorns and their descendants in these experiments, but is more common in the Hamburgh breed. (Hamburgh mode.)

These six grades of colour shades in eggs are apparently continuous, but the experiments show a genetic discontinuity between the mode-grades 3 and 2, with some indications of other grades breeding true suggesting the presence of subfactors for intensity of tint.

The results, however, are complicated by the fact that though the darker shades always seem to be dominant over the lighter shades, yet the cross-breds appear to be intermediate in tint between the two

extremes, consequently there may be considerable external complexity through over-lapping, *e.g.*, Brown (grade 3) \times White (grade 1) gives White (grade 2), thus *apparently* reversing the dominance of Brown over White.

There is no doubt that this apparent intermediacy is due, in some cases at least, to the hybrid nature of the darker grades, which are carrying the recessive subfactors for the lighter grades.

In these experiments each egg laid by the hen during her first year's laying was graded by comparison with a set of fresh eggs representing the six colour shades. After a little practice no difficulty was experienced in grading these instantly by the eye.

It was found that egg-colour was much less variable in the individual hen than egg-size. The individual White Leghorn, as a rule, laid one or two grades only during the year, while the individual White Wyandotte usually laid two or three grades. Unlike egg-size, little or no seasonal variation was found in egg-colour.

The mode colour grade of the year, *i.e.*, the colour grade with the largest number of eggs, was taken to represent the egg-colour of the individual hen.

Mode-grades 5 to 3 inclusive are classed as Brown (C) and mode-grades 2 to 0 inclusive as White (c).

Table VII gives a summary of the results of the various matings, and out of 331 daughters there were 137 Brown (C) and 194 White (c), while the Mendelian expectation was 142.00 Brown (C) and 189.00 White (c). There were two definite exceptions, namely:—

(1) W 726 [W 535 (Cc3) \times W 554 (CC)] produced 79 eggs up to April 20th, 1916, of colour-mode grade 2, *i.e.*, one grade lighter than expected. Her five sisters had a colour-mode of grade 3 as expected, and 22 other daughters of W 554 had colour-modes of grades 3 and 4.

(2) W 194 [W 3 (cc2) \times W 7 (CC)] produced 92 eggs from March 1st, to October 31st, 1913, of colour-mode grade 2, *i.e.*, one grade lighter than expected. Her ten sisters had colour-modes of grade 3, as expected.

It is possible that these rare exceptions were due directly or indirectly to external conditions or to incomplete dominance.

Out of 64 Leghorns tested genetically all were cc, while of 52 Wyandottes, there were 24 CC, 22 Cc, and 6 cc. The colour-mode of all the Leghorns was grade 1 (White), while the colour-mode of all the Wyandottes was grade 3 (Brown).

These results confirm the previous experiments of the author with

TABLE VII. C FACTOR. EGG-COLOUR.

(a) *Daughters Sired by White Leghorns.*

Matings			Offspring		E.C.M. Grades (Dark Brown 5 to Chalk White 0)							Observed		Calculated	
Sires		Dams	Daughters		Brown			White				Brown		White	
Nos.	Factors	Nos.	Factors	Nos.	5	4	3	2	1	0		Brown	White	Brown	White
1	cc	1	Cc	15	—	—	—	6	3	—		6	9	7.50	7.50
11	cc	45	cc	135	—	—	—	—	8	87	40	0	135	0.00	135.00
12	—	46	—	150	—	—	—	6	14	90	40	6	144	7.50	142.50

(b) *Daughters Sired by White Wyandottes.*

Sires		Dams	Daughters		Brown			White				Brown		White	
Nos.	Factors	Nos.	Factors	Nos.	5	4	3	2	1	0		Brown	White	Brown	White
2	CC	4	CC	20	2	4	14	—	—	—		20	0	20.00	0.00
1	CC	2	Cc	7	—	—	6	1	—	—		6	1	7.00	0.00
3	Cc	16	CC	41	1	15	25	—	—	—		41	0	41.00	0.00
1	CC	1	cc	11	—	—	—	1	—	—		10	1	11.00	0.00
4	Cc	6	Cc	38	—	—	11	18	9	—		29	9	28.50	9.50
5	Cc	7	cc	51	—	—	25	25	1	—		25	26	25.50	25.50
1	Cc	1	Cc	3	—	—	—	3	—	—		0	3	1.50	1.50
2	cc	2	cc	10	—	—	—	—	10	—		0	10	0.00	10.00
19	—	39	—	181	3	30	98	39	11	—		131	50	134.50	46.50

(c) *Daughters Sired by White Leghorns and White Wyandottes.*

Matings			Offspring		E.C.M. Grades (Dark Brown 5 to Chalk White 0)						Observed		Calculated	
Sires		Dams	Daughters		Brown			White			Brown	White	Brown	White
Nos.	Factors	Nos.	Factors	Nos.	5	4	3	2	1	0	Brown	White	Brown	White
2	CC	4	CC	20	2	4	14	—	—	—	20	0	20·00	0·00
1	CC	2	Cc	7	—	—	6	1	—	—	6	1	7·00	0·00
3	Cc	16	CC	41	1	15	25	—	—	—	41	0	41·00	0·00
1	CC	1	cc	11	—	—	10	1	—	—	10	1	11·00	0·00
4	Cc	6	Cc	38	—	11	18	9	—	—	29	9	28·50	9·50
5	Cc	7	cc	51	—	—	25	25	1	—	25	26	25·50	25·50
2	cc	2	Cc	18	—	—	6	9	3	—	6	12	9·00	9·00
13	cc	47	cc	145	—	—	—	8	97	40	0	145	0·00	145·00
31	—	85	—	331	3	30	104	53	101	40	137	194	142·00	189·00

Mendelian expectations: A—all Brown; B—3 Brown : 1 White; C—1 Brown : 1 White; D—all White.

Buff-Cochins, Black Hamburgs, White Leghorns and Houdans (Hurst, 1905) (see p. 219) in which Brown egg-colour was found to be dominant to White egg-colour in F_1 (1st generation), and now extend the observations to F_2 and F_3 (2nd and 3rd generations), showing the segregation and gametic purity of the factors C and c concerned. As an illustration a single case is detailed, as follows:—

Two White Leghorn hens L 5 (cc) and L 21 (cc) were mated with a White Wyandotte cock (W 10 (Cc)), giving 30 daughters, of which 13 laid Brown eggs (Cc) and 17 laid White eggs (cc). Two of the Leghorn-Wyandotte daughters, WL 48 (cc) and WL 53 (cc) were mated back to two White Leghorn cocks, L 578 (cc) and L 579 (cc), giving 12 daughters, all of which laid White eggs (cc).

In this case the first-cross was *apparently* intermediate, giving a continuous series of Light Browns, Creams and Ivory White, yet genetically the Light Browns and Creams proved to be discontinuous.

Since the above factorial scheme was worked out important data on the inheritance of egg-colour in Langshan, Brown Leghorn, and Gold Pencilled Hamburg crosses have been published in the *Journal of Genetics* (Punnett and Bailey, 1920). On the whole, the results seem to be similar to the Wyandotte and Leghorn results given above, and although no precise factorial analysis was attempted in the Cambridge experiments owing to the insufficient data available, there can be no doubt that the general facts described by Punnett, and his suggested interpretation of the same, fit the C factor scheme worked out above for Wyandottes and Leghorns. For instance, the F_2 of Langshan ♀ × *Hamborough* ♂ and Langshan ♀ × *Brown Leghorn* ♂ give numbers approximating to the 3 Brown : 1 White expected, and the F_2 of (Langshan-Hamborough) ♂ × *Hamborough* ♀ gives numbers near to the expected equality.

On the other hand, the reverse cross *Brown Leghorn* ♀ × *Langshan* ♂ gave in F_2 a great excess of White eggs. Punnett suggests that this may indicate the presence in the *Brown Leghorn* dam of a factor for the inhibition of pigmentation in the eggs. Expressed in factors, if C is the pigmentation factor and J its inhibitor, then the mating would be *Brown Leghorn* (ccJJ) ♀ × *Langshan* (CCjj) ♂, F_1 birds would be CcJj, and the F_2 ratio would be 9 CJ : 3 Cj : 3 cJ : 1 cj, or 3 Brown : 13 White. It is evident that Punnett's suggestion adequately explains the excess of White eggs in the F_2 of this mating, and it may be that this is the correct interpretation of the facts. At the same time, in the light of my results with Wyandotte × Leghorn, I rather incline to the more simple

interpretation in this case that the Langshan cock used was heterozygous (Cc), giving a mixed F_1 , of Cc and cc birds, and that a chance excess of cc birds in the few mated gave the excess of White eggs observed in F_2 . This suggestion would explain the White eggs laid by the F_1 hens in this mating, and also bring into line Punnett's interesting observations on the association in this mating of black down with White eggs. It is, of course, not impossible that both schemes may be working simultaneously in the same material, but it is hardly likely in this case because that would involve a much greater excess of White eggs in F_2 (about 8 : 1 instead of the 3 : 1 observed). It is hoped that someone with the necessary resources will undertake some crucial experiments in the near future to determine the limitations of the above suggestions. In that case it may assist the student if a brief comparison is made between the egg-colour grades used independently in the two sets of experiments at Cambridge and Burbage. The Cambridge grades (CG) of egg-colour are 12 in number, and are based on the standard colour charts published in the *Répertoire de Couleurs* (Dauthenay, 1905). The selected grades are somewhat unequal in their differences of intensity of tint, and frequently more than one colour-chart is utilised to determine the grade, otherwise the standard is excellent, and, above all, constitutes a permanent record.

The Burbage Grades (BG) of egg-colour are, as we have seen, 6 in number and are based on sets of fresh eggs of the 6 selected grades, each with an equal difference of intensity of tint: the 6 grades are easy to memorise as the mode-grades of certain breeds, and to recognise at sight. One disadvantage found was that it was necessary to renew them frequently as they fade rather quickly when exposed to light, and, further, there is no permanent record possible. It may be useful, therefore, to place on record here their equivalents in the more permanent C.G.:—

B.G. 0 (Hamburg Mode)	equivalent to	C.G. 1.
B.G. 1 (Leghorn)	C.G. 2 and 3.
B.G. 2 (Game)	C.G. 4 and 5.
B.G. 3 (Wyandotte)	C.G. 6 to 9.
B.G. 4 (Cochin)	C.G. 10 and 11.
B.G. 5 (Rhode)	C.G. 12.

It should be noted, however, that in one respect the two standards are not strictly comparable, because in B.G. the superposed partial "pinkness" in the 2, 3 and 4 grades was deliberately excluded, the Brown or Cream ground-colour alone being taken in determining the grade, the "pinkness," when present, was simply recorded as P, and

added to the grade. It is evident that the "pinkiness" is due to a genetic factor (P) distinct from the factor for the ground-colour of the shell (C), but its genetics has not been worked out. On the other hand, in C.G., the "pinkiness" is included with the Brown and Cream ground-colours, and this, no doubt, explains why C.G. 6—9 are equivalent to B.G. 3 and 3 P. For that reason there is a slight doubt about the precise genetic position of C.G. 5, which I believe is equivalent to B.G. 2 P. This point is important because, as we have seen, the genetic division line lies between B.G. 2, which is White, and B.G. 3 which is Brown, C.G. 4 is undoubtedly B.G. 2 and is genetically White, while C.G. 6 is undoubtedly B.G. 3, and is genetically Brown. For the present we may, I think, regard C.G. 5 as equivalent to B.G. 2 P, and consequently genetically White, but the possibility of its being otherwise should be borne in mind.

With regard to the different terminology used in the two sets of experiments, it is clear that Punnett's "Major factor leading to increased tint of egg" is the same as my "C. Factor," while his "Minor factors" no doubt correspond with my "Sub-factors."

In conclusion, it may be said that although the complicated problem of the inheritance of egg-colour in poultry has not yet been fully worked out, the close agreement, both in the results and in their interpretation, in the two sets of experiments which were carried on independently, with ten different breeds and in different districts, make it almost certain that the ultimate solution of the problem will be found on these lines, and it is unfortunate that both sets of experiments had to be abandoned on account of the War.

(10) SUMMARY AND DISCUSSION OF RESULTS.

Six years' experimental breeding and testing on Mendelian lines show that the first year's egg-production of a hen depends on the combined action and reaction of many genetic factors.

Seven main factors have been identified in the Utility strains of White Leghorns and White Wyandottes used.

One of these C, influences egg-colour, another N, influences egg-size, and five (E W S M and H) control egg-number. Of these, E and W together determine winter production, S is manifested in spring and early summer production, and M in late summer and autumn production, while H may affect the production of any of the three periods.

Pearl's discovery of two genetic factors for winter production in Plymouth Rocks, confirmed by Goodale in Rhode Island Reds, is further confirmed in White Leghorns and White Wyandottes.

It is possible that Pearl's factors L_1 and L_2 for winter production in Plymouth Rocks, Goodale's factors A and B for winter production in Rhode Island Reds, and the writer's factors E and W for winter production in White Leghorns and White Wyandottes are identical, but it is not certain. For neither Pearl's nor Goodale's factors are individually identified with Sexual Maturity (E) or with rate of winter production (W), and as Pearl's L_2 factor is sex-linked while the others are not, it seems impossible to identify E and W definitely either with Pearl's L_1 and L_2 , or with Goodale's A and B factors.

Tables I. to VII. give summaries of the results of the matings in White Leghorns and White Wyandottes for each of the seven genetic factors concerned, and, on the whole, the totals show a general fitness with the Mendelian ratios expected. Reducing the results of the seven Tables to terms of Mendelian Dominants and Recessives (Table VIII.), the total numbers observed are 1195 D : 687 R showing a deficiency of 17.75 Dominants and a corresponding excess of Recessives in the total of 1882, or less than 1 per cent. Eighteen definite exceptions are discussed in detail: 2 of these proved to be somatic and not genetic exceptions; 11 are slight exceptions, probably of the same nature; 3 are pathological; 1 is possibly an incomplete Dominant, while one is apparently a true mutation.

TABLE VIII.

Summary of results in White Leghorns and White Wyandottes.

Characters	Totals	Dominant	Observed	Calculated	Recessive	Observed	Calculated
Sexual Maturity	335	Early (E)	286	289.00	Late (e)	49	46.00
Winter Rate ...	266	Fast (W)	231	231.75	Slow (w)	35	34.25
Spring Rate ...	224	Fast (S)	216	217.25	Slow (s)	8	6.75
Autumn Rate ...	194	Slow (M)	140	145.50	Fast (m)	54	48.50
Broodiness ...	201	Broody (H)	50	58.50	Non-B. (h)	151	142.50
Egg-size ...	331	Small (N)	135	128.75	Large (n)	196	202.25
Egg-colour ¹ ...	331	Brown (C)	137	142.00	White (c)	194	189.00
Totals ...	1882	—	1195	1212.75	—	687	669.25

The seven factors and their allelomorphs appear to segregate in the normal Mendelian manner, and so far as the present data go, each factor

seems to be independent of the others in their assortment in gametogenesis with no evidence of linkage or crossing over, but the numbers derived from the crucial matings are too small to decide this point satisfactorily.

SEX-LINKAGE.

There is no evidence of sex-linkage in the data, though in one case (Factor W in White Leghorns) a large excess of heterozygous females was observed with a corresponding deficiency of homozygous females. (See Table II.) All the seven factors appear to be handed on equally to sons and daughters by sires and dams.

Pearl's discovery that one of the winter-production factors was sex-linked in the female, in Plymouth Rocks, is apparently not applicable to the White Leghorns and White Wyandottes used, which, on the contrary, resemble Goodale's Rhode Island Reds in this respect.

In view of this, it seems probable that the Barred Plymouth Rock is exceptional in its sex-linkage of one of the factors for Winter egg-production, and it is not impossible that this may be due to the linkage of the egg-production factor with the factor for Barred plumage which is one of the classic cases of sex-linkage. If that is so, individual White Leghorns or White Wyandottes carrying the sex-linked factor for Barred plumage (cf. Hurst, 1905) (see p. 232), might be expected to follow Pearl's scheme of a sex-linked factor for winter egg-production.

No case of a Leghorn or Wyandotte hen carrying the Barred factor was met with in these later experiments, though a single case of a Leghorn cock was observed.

GENETICS AND SOMATICS OF EGG-PRODUCTION.

For a high annual production, a high winter-production is necessary, and this is only attained in the presence of both E and W factors. In the absence of either E or W, or both (Ew, eW or ew) a low winter-production results in White Leghorns and White Wyandottes, *if the pullets are hatched at a normal time*. If, however, the pullets are hatched abnormally *early* Ew and eW birds may have a high winter-production; on the other hand, if the pullets are hatched abnormally *late*, EW birds may have a low winter-production; while ew birds will usually have a low winter-production unless they are hatched very early indeed.

For a maximum annual production the presence of the E, W, and S factors and the absence of the M and H factors are necessary, while for a maximum annual production of large eggs the factor N must be absent

too. For the highest numerical production it is also necessary for the dominant factors to be present in a homozygous state. So that the genetic formula for the highest annual producer is EEWWSSmmhh, while that of the lowest producer is eewwssMMHH.

Judging by the results obtained in these experiments, the annual records of the highest producers normally range from about 200 to 300 eggs according to the external conditions, while that of the lowest producers normally range from about 50 to 75 eggs. Between the highest and the lowest annual production there is every possible numerical record between 50 and 300, depending mainly on the presence or absence of any of the five genetic factors for production.

SELECTION VALUE OF NUMERICAL RECORDS.

From this it follows that the annual numerical record may be due to various unknown combinations of factors, and consequently has little, if any, selection value, except in the case of the two extremes 50 and 300 whose factorial constitutions are obvious.

It is evident therefore that the Selection Value of a numerical record between 100 and 200 eggs is very slight.

MASS SELECTION AND PEDIGREE SELECTION.

A comparison between the genetic constitutions of the three strains of Leghorns and Wyandottes used in the experiments is instructive. For instance, taking the four chief factors of egg-production E W S M, the genetic constitutions for a maximum production, are as we have seen, EEWWSSmm.

The percentages of birds of these constitutions found in the three original strains used in the experiments were as follows:—

No. 1 Strain.—(Mass Selection) EE, 0·0°/°; WW, 0·00°/°; SS, 94·1°/°; mm, 0·0°/°.

No. 2 Strain.—(Pedigreed for two generations): EE, 14·2°/°; WW, 28·5°/°; SS, 57·1°/°; mm, 16·6°/°.

No. 3 Strain.—(Pedigreed for three generations): EE, 36·3°/°; WW, 36·3°/°; SS, 54·5°/°; mm, 45·4°/°.

The above figures explain themselves, and illustrate the results of different methods of selection.

It is evident that No. 1 strain was let down badly in a single season (1910) by the use of an eewwSsMM cockerel, showing the disadvantages and risks of Mass selection. Nos. 2 and 3 strains show the advantages of pedigree breeding and trap nesting, but the objective of the selection

is far from being attained, owing obviously to the genetic factors of egg-production being unknown at that time. The practical proof of this lies in the fact that homozygous strains of EEWSSmmnn birds were bred in 1914 at Burbage, which were extractions of the heterozygous pedigree strains united in 1910.

Since the War, other pedigree strains and other breeds have been tested with success at Burbage and elsewhere on the basis of the above factorial scheme.

SOMATIC AND GENETICAL SYSTEM OF CLASSIFICATION.

In order to analyse the continuous data of egg-production a special system of uniform gradings was adopted, which led eventually to the identification of the seven genetic factors. The old method of grading layers by their winter or annual numerical records was found to be inadequate and unreliable as a measure of egg-production on account of its dependence on external conditions, *e.g.*, date of hatching. In place of this a system of uniform percentage-gradings was adopted to express the Rate of Egg-Production of each individual hen in winter, spring and autumn respectively.

A uniform system of grading was also used for Sexual-Maturity, Broodiness, and Size and Colour of Eggs, and the Somatic grading was based throughout on the genetic factors concerned.

In this way, each individual hen tested for egg-production, was given a Somatic formula to show her Somatic grading in the genetic factor concerned.

Each Sire and Dam tested had the usual genetic formula to which, in the case of the dam, was added her Somatic grading.

INCOMPLETE DOMINANCE.

In all the factors (except H) Dominance tends to be incomplete and the heterozygotes are more or less intermediate. The intermediacy is, as a rule, expressed in the form of a less extreme grade of dominant, which does not overlap the recessive grades (except occasionally with N and C factors).

In some cases it is possible to recognise the homozygous dominants by their extreme grades, though not always.

ECONOMIC SIGNIFICANCE.

It is obvious that these genetical results are of considerable economic importance, and the possibilities of their application to practical poultry breeding, will now be dealt with.

(11) BREEDING FOR EGG-PRODUCTION.

A precise knowledge of the genetic factors concerned in egg-production will enable the pedigree poultry breeder to raise homozygous strains of various breeds which will not only produce a maximum supply of eggs, but, more important still, may be relied on to breed true to this high standard.

It is hoped that the genetic data now published will provide the pedigree breeder with a foundation on which he can build up and *keep going* a high producing strain of birds. It is true that many breeders have already achieved remarkable results with their strains by industry, perseverance in selection, and good luck. But in few cases can they say how it was done, nor are they certain that they can repeat the result at any given time, consequently their strains may run out at any season, and it may take years to establish them again by the old methods.

On the other hand, by applying a knowledge of the genetic factors concerned, the pedigree breeder can re-make his strain with certainty in a given time, and, what is more important, *can keep it going when he has got it*. All that is required is an elementary knowledge of Mendelism, together with the list of genetic factors concerned in egg-production, published in this paper. A few general remarks on the application of genetics to poultry breeding may also be useful.

PULLET YEAR THE MOST IMPORTANT.

First it will be observed that these genetic factors only apply to the egg-production of the pullet's first year of laying, which after all is the most important period. Only the breeders have been kept more than one season in these experiments, but as a rule it was found that the second year's production of each hen was, on the average, about 60 per cent. of the first year's production, while the third year's production was about 40 per cent. of the first year's production. In every case the second year's production was less than the first, and the third year's production less than the second. The first year's production is, therefore, of the greatest importance. Genetically this is divided into three distinct periods: winter-production, from first egg to February 28th or 29th; spring-production from March 1st to June 30th; and autumn-production from July 1st to end of laying year. Of these three production periods, it is generally admitted that the winter-production is most important, for obvious reasons.

HOW TO SECURE HIGH WINTER-PRODUCTION.

For high winter-production there are at least two genetic factors concerned, E (Early Maturity) and W (Fast Rate), and it is necessary that both these factors should be present together in the pullet. The e (Late Maturity) and w (Slow Rate) factors are not wanted, and any birds containing them must be discarded. Thus Early-Slow (Ew) and Late-Fast (eW) birds are equally useless, and only the Early-Fast (EW) birds must be retained. These will be good winter-layers. But genetically there are four kinds of Early-Fast (EW) birds, and not all will breed alike. These are Double-Early Double-Fast (EEWW), Single-Early Double-Fast (EeWW), Double-Early Single-Fast (EEWw), and Single-Early Single-Fast (EeWw), of these only the first (EEWW) is any use for a permanent strain, all the others will let down the breeder in a generation or two and, though all are themselves good layers, they must be discarded for breeding purposes, in spite of their high winter-records. On the other hand, the EEWW birds are not only high-producers, but they will *breed* high-producers.

The problem is to find out which are the EEWW pullets. As both factors are dominant the easiest and quickest method is to test them by mating with the double recessive (eeww), *i.e.*, any cockerel of a breed known to be Late-Maturers and Slow Winter-Layers.

For this purpose I have found a Cumberland strain of the Old English Pit Game (still bred solely for cock-fighting) the most useful. If *any* late (ee) or slow (ww) birds come from this mating, the mother must be discarded. If, however, all her daughters are Early-Maturers and Fast Winter-Layers the mother tested is EEWW, and can be used in the breeding pen as soon as the test is completed. (If necessary the test for W can be taken to February 1st instead of March 1st, which gives ample time.) Precisely the same remarks apply to the cockerels as the pullets. Only the EEWW birds should be used, and they should be tested with eeww hens, and used for breeding the following season as cocks, if they prove to be EEWW. Once the breeding pen of both sexes has been tested, and found to be EEWW no further test is required, so far as they are concerned, nor will any of their offspring pullets or cockerels require to be tested at all, for they should all be EEWW, if the original test was made correctly. It will, of course, be understood that the above remarks apply more especially to White Leghorns and White Wyandottes, though I suspect that Rhode Island Reds are in the same category, judging by Goodale's experiments. For Plymouth Rocks a different test result may be expected, for the pullets,

according to Pearl's results cannot be EEWW, and the best one can get will be EEWw or EeWW, owing to sex-linkage.

HIGH SPRING- AND AUTUMN-PRODUCTION.

For high spring-production, only one genetic dominant factor is concerned (S), and the SS bird, cock or hen, is the one required. This factor is not so important as the others, as most hens lay well in the spring and early summer, and are SS, at the same time it is necessary that no Ss birds are used, because they will give rise to ss birds, which are useless. If any of these appear their parents should be discarded as breeders.

No direct test for the S factor is usually available owing to the rarity of ss birds of either sex. The Pit Game is usually SS.

For high autumn-production the case is somewhat different from both winter and spring production inasmuch as it is the recessive factor mm that is required, and not the dominant M, which gives slow-production, consequently no testing is necessary, as the mm hens are known definitely by their performance as autumn-layers. As a rule it will be found that the mm birds do not fall into a deep moult in the autumn like the ordinary MM and Mm birds, but gradually shed a few feathers and keep on laying, often for 13 or 14 months after the first egg. With regard to the cockerels, it is difficult to test for mm, because if a cockerel was tested with mm hens and all his daughters were mm, he would be mm, but he could not be used for breeding until his third season. Probably the best method would be to breed cockerels from mm hens only for several generations, and if he threw M birds discard him and try another until an mm was secured. Once secured the strain would be fixed. So far, I have found the Pit Game always to be MM, so that it is no use for this test.

ELIMINATING BROODINESS.

The fifth and last genetic factor influencing a high yearly production is the presence (H) or absence (h) of broodiness. Here again it is the recessive hh, or Non-broody bird that is required, as broody birds (HH or Hh) reduce the spring and autumn productions, and sometimes the winter production also. In other words the factor H acts as a partial inhibitor to factors W, S and m, preventing their full expression. Owing to the fact that broodiness sometimes does not show itself until the second or third laying season, first season Non-broodies may in reality be broody Hh, and the problem of the elimination of

broodiness in a strain is therefore a difficult one, probably the most difficult one that the poultry breeder has to face.

The best method is to breed from hens that have shown no signs of broodiness during their first year's laying, and discard them and their progeny at once if they go broody later: as only about one in six do this, it is not a very serious matter. The selection of the hh cock is the greater difficulty, for to test his daughters for broodiness for two or three years would mean that he could not be used for breeding until his fourth or fifth season, which is rather impracticable. The best course to take would probably be to breed all cockerels from two and three year Non-broodies for several generations, use him for breeding as a cockerel, and discard him as soon as it is found he has thrown a broody daughter. If he does not, he is hh, and a prize indeed.

THE FIVE IMPORTANT FACTORS.

From the above remarks it will be observed that the first year's egg-production of a pullet depends on at least five genetic factors, which, independent in their inheritance, and following Mendel's Laws in their segregation and assortment, yet act and re-act upon one another with various results in egg-production. For a maximum egg-production the hen should be carrying the following five factors at least, EWSmh.

In these experiments under ordinary conditions of feeding, housing and management EWSmh hens gave first year records of 192 to 254 eggs.

In the hands of an expert poultryman, and under optimum conditions, the same hens would, no doubt, have averaged 250 each or more.

If we suppose for simplicity of calculation that the five genetic factors are of equal value in egg-production, then each would be responsible, say, for 50 eggs of the record. Now if *any one* of the five factors was absent, the year's record would be 200 eggs instead of 250, so that a record of 200 eggs might be produced by five differently constituted hens, viz.: eWSmh, EwSmh, EWsmh, EWSMh or EWSmH. Similarly if *any two* of the five factors were absent, the year's record would be 150, instead of 250, so that a record of 150 eggs might be produced by *ten* differently constituted hens.

It is evident, therefore, that the egg-record alone of a hen is not of much value as a guide to the genetic constitution for egg-production: at the same time, it is obvious that the higher records from 200 to 250 are of more selection value than the lower records from 150 to 200; for

a record of 250 shows that the hen is carrying most, if not all, of the genetic factors of egg-production, while a record of 150 shows that some at least are missing. Many of our best breeders realise this by breeding only from the highest records.

On the other hand, it seems to be a popular idea in England among certain breeders, that it is an error to breed from hens with the highest records, and that those with medium records are to be preferred.

A study of the genetic factors of egg-production gives no support to the latter doctrine, everything else being equal.

BREED FROM BIRDS WITH HIGHEST RECORDS.

Any departure from the old rule of breeding from the highest record is bound to lead to a lower egg-production. Cases of reduced fertility and vigour in high producing hens were not met with in the experiments; on the contrary, the high producers on the whole were far superior to the low producers in both fertility and vigour. Indeed, it was found difficult to breed and rear pullets to Maturity from the low producers, *e.g.* Zero birds, and those with a first year's record of under 100.

Another point of considerable practical importance is that in the case of all the factors concerned in egg-production, the dominance was almost always incomplete, and the heterozygotes were apparently more or less intermediate.

Consequently it is possible generally to recognise almost with certainty the Double-Dominants from the Single-Dominants without testing them. This knowledge will be useful to the small breeder with limited resources who has neither the means nor the room for testing birds genetically on a large scale. At the same time it must be said that for absolute certainty, the progeny test is the only reliable method.

The fact that the Double-Dominant produces a superior grade to the Single-Dominant, is also a point in favour of the selection of high records for breeding, because the higher the record, the more superior the grade of the factors concerned, and the more superior the grade the more likely is the individual to be homozygous or true breeding.

This also brings out the great practical value to the breeder of a system of definite grading in all the characters concerned in egg-production.

Altogether, apart from the question of Genetics, a system of definite grading, similar to that presented in this paper, will, it is hoped, be found useful for descriptive and classification purposes in all the characters concerned in egg-production. Perhaps it is not too much to expect

that this system will supersede the present methods of grading layers according to their annual or winter records which we have shown to be of little value, as they only lead to confusion and the mixing up of totally different things.

Take the winter record for instance, which we have seen depends genetically on the factors E and W, and which, in addition, somatically depends on the date of hatching. It is much more precise and useful to say that a hen is E6W6 than to say that her winter record is 50. E6W6 signifies at a glance that the hen matured at from 6—7 months old, and laid during the winter at a rate of 60 to 70 per cent., and being of a superior grade is likely to be a true breeder.

On the other hand, a winter record of 50 might mean many things. It might mean, for instance, an Early Maturing Slow-layer (Ew), a Late Maturing Fast-layer (eW), it might even be a very early hatched Late Maturing Slow-layer (ew), or it might be what it is usually intended to mean, a good winter-layer (EW). All things are possible to a winter record in early hatchings.

Further an E6W6 hen might have a winter record of over 100, or only 30, according to the date of hatching and the conditions under which it was raised, but in either case it is equally valuable as a breeder.

DANGERS OF EARLY HATCHING.

From this it follows that the modern demand for early-hatched pullets for egg-production may prove to be a delusion and a snare to the breeder. Early hatching naturally produces higher winter records and higher annual records, but at the same time in so doing it may mislead and deceive the breeder by obscuring the genetic constitution of his birds. If hatched early enough Ew and eW, and even ew birds may put up a high winter record, but as breeders they are useless as they only simulate the EEWW birds which are the only true breeders and layers. The adoption of the new system of percentage gradings for E and W will avoid this modern danger.

The same remarks apply to the year's record, which, as we have seen, is of doubtful value if under 200 eggs, as an identical record may be made by many different kinds of hens, each having a different breeding value.

WINTER AND ANNUAL RECORDS OF PRODUCTION MISLEADING.

In the light of genetics it is evident that the present methods of grading layers simply by their records of winter production or annual

production, are inadequate and in most cases misleading to the breeder. On the other hand the adoption of a system of precise grading of the performance of each bird in each of the six important genetic factors concerned in egg-production, on similar lines to that now presented, would undoubtedly be a great advantage from many points of view. If, for instance, the system were adopted in the various Laying Competitions, in place of the somewhat cumbersome and variable conditions under which they are now running, more interest still might be taken in them by the breeder, and the competition and rivalry would be more keen to see who could breed a perfect pen of superior grades in *each* of the laying factors, and the authorities who run these competitions would have the satisfaction of knowing that the winning birds would also be certain to breed winners, which is not so at present. In this way rapid progress would be made in the science and art of Poultry Breeding.

VALUE IN LAYING COMPETITIONS.

The adoption of a genetic system of the classification of layers in the Annual Laying Competitions would also prove of considerable educational value to the general Poultry-keeper, who follows the details of the competitions with keen interest.

The methods adopted of recording the eggs would be practically the same, the only difference would be in the calculation and presentation of the results. Another important advantage to Poultry-Breeders would incidentally arise, and that is the abandonment of the reduction of the laying-year to 48 weeks, which for convenience has lately been adopted in England. Genetically this change is unfortunate, in view of the fact that the recent increased records up to 300 and over may be distinctly traced to the appearance of the recessive mutation (*m*) which by inhibiting the deep autumn moult increases the biological year of the layer to 13 or 14 months. Genetically it would appear desirable to extend the Annual Laying Competition to 56 weeks or 400 days, rather than reduce them to 48 weeks, as the adoption of the latter course tends to reduce egg-production through the non-elimination of the Deep Moulters (*MM* and *Mm*).

INCREASING EGG-SIZE.

The sixth genetic factor *N*, which determines the size of egg, is a most important one, in egg-production, especially in the White Wyandotte. Here again it is the recessive *nn* that is required to produce large eggs. Many breeders seem to think if they set or incubate large

eggs only, that solves the problem, but this is far from being the case. These experiments show clearly that it is the large-egg *mode* (n) that is important. Many hens lay a few large eggs, but have a small-egg mode (N). In such a case her large eggs would only breed pullets with a small-egg mode like herself, everything else being equal. Large-egg mode being a simple recessive character (nn) breeds true, the nn hens are easily selected by their performance, and the only difficulty is to secure the nn cocks.

Cockerels should only be bred from large-egg mode hens for several generations, and tested as cockerels with nn hens; if any of the daughters have a small-egg mode they should not be used for breeding in their second season as cocks. On the other hand, if all their daughters have a large-egg mode they are nn , and can be used for breeding, giving rise to a permanent strain which under normal conditions will not change.

Several striking cases of this were found in these experiments, and a large-egg strain of White Wyandottes was established at the time of the outbreak of the War.

FIXING EGG-COLOUR.

The seventh and last factor to be considered is that of egg-colour (C). This is not strictly a production factor, perhaps, nor is it in England of much economic importance. It is, however, of some interest elsewhere, inasmuch as in America I understand that White eggs are usually preferred to Brown ones. In any case, it is possible to breed either White or Brown eggs as desired, remembering that Brown (C) is dominant and White (c) recessive, and that different grades of each when crossed tend to be intermediate in tint.

If a true breeding Brown-egg race is desired, the factorial constitution will be CC , and if a White egg-race it will be cc . The cock, of course, carries these factors, as well as the hen, though he cannot give expression to them.

The system of grading layers presented here has a double value to the practical breeder, because the descriptive somatic gradings are based throughout on the genetic factors concerned, thus giving the breeder a line also to the breeding value of each bird graded, for, as we have seen, the extreme grades tend to breed true.

(12) CONCLUSION.

EVOLUTIONARY SIGNIFICANCE.

From an evolutionary point of view the genetic results are significant, inasmuch as they serve to indicate the gradual evolution of the increase of fecundity in the domestic hen by means of a succession of definite and discontinuous steps or mutations.

Seven of these steps have been investigated genetically, and it will be observed that with regard to six of them three are dominant and three are recessive mutations. The dominant mutations are Early Maturity (E), Fast Rate of Winter Production (W), and Fast Rate of Spring Production (S); while the recessive mutations are Fast Rate of Autumn Production (a), Non-broodiness (h), and Large Eggs (n). With regard to the seventh factor for egg-colour (C), there is an element of doubt as to whether a dominant or a recessive mutation is involved, inasmuch as it is not clear whether the Asiatic breeds laying brown eggs were or were not derived from the same source as the Mediterranean breeds laying white eggs.

A single case of the solitary occurrence of a recessive mutation was observed in the experiments, which apparently originated in a male Wyandotte by the absence of the factor (N) (Small-Egg mode) in a single gametogenesis, giving rise to a daughter and grand-daughters with large-egg modes (n). It is possible that the original mutation (n) arose in the same way in the wild species or under early domestication, though in that case at least two generations would elapse before it could appear, owing to its recessive nature and the lack of a recessive mate.

In many respects this mutation for large-egg mode seems analogous to the mutation of the Spencer Sweet Pea.

The recessive mutation (m) is of comparatively recent origin, while the dominant mutation (W) has apparently arisen during the last fifty years. The dominant mutation (S) and the recessive mutation (n) must have originated at a much earlier date.

The dominant mutation E and the recessive mutation (h) (or dominant I) apparently arose among the Mediterranean breeds.

GENETICAL SIGNIFICANCE.

To the student of Genetics the chief interest in the investigation will be the attempt to analyse genetically a complex and continuous physiological character that is manifested in one sex only (consequently

presenting small numbers) and which is obviously influenced to a considerable extent by the changing conditions of life.

The unequal influences of the external conditions were minimised by the adoption of certain uniform methods of housing, feeding and exercise, which involved the keeping of each individual hen in a single house and run, and consequently entailed extensive plant and labour.

The complex and continuous nature of the character investigated necessitated the formulation of a special system of uniform character-gradings, which eventually led to the identification of the genetic factors concerned. The almost insuperable difficulty of the small numbers in the families was eventually overcome by reversing the ordinary order of genetic analysis, and the genetic constitutions of the birds were ascertained mainly by means of a combination of Somatic, Parental and Progeny Qualitative tests rather than by the usual Progeny Quantitative test. This combination method of analysis may possibly prove useful to others who have to deal with the incidence of small families in the larger animals and Man. Apparently complex, it is really simple and at the same time critical, for the harmony of its complexities signifies its soundness.

Some interesting and uncommon Mendelian Ratios were met with in working out the HI scheme for broodiness, in which the presence of a dominant inhibitor I inhibits a second dominant factor H. In addition to the ordinary ratios of 3 : 1 and 1 : 1, there also appear ratios of 1 : 3, 1 : 7, 3 : 5, and 3 : 13. This scheme fits most of the data for broodiness in poultry so far reported, but experiments on a large scale are required to demonstrate it adequately.

In each of the seven genetic factors for egg-production there are distinct indications of the presence of one or more sub-factors for increased production, but the numbers are insufficient to determine these and their allelomorphs precisely. It is probable that an intensive study of a single set of the sub-factors would throw some light on the nature of the "Fractional Factors" of Bateson (1914) and the "Multiple Allelomorphs" of Sturtevant (1913) and others (cf. Hurst, 1913). (See p. 457.)

In view of the recent important contributions to the chromosome theory of the mechanism of heredity by Morgan and his colleagues (Morgan, 1919), it is unfortunate that the experimental matings made are for the most part unsuitable for testing the possible linkages of the seven production-factors, consequently the numbers are too small in the crucial matings to test the question satisfactorily. Investigations in this

direction might lead to results of considerable genetic and economic importance.

REFERENCES TO AUTHORS AND LITERATURE.

- BATESON, W. (1913). *Mendel's Principles of Heredity*. (Cambridge.)
 — (1914). *Presidential Address to British Association for the Advancement of Science* (Australia).
 BATESON, W. AND PUNNETT, R. C. (1911). The Inheritance of the Peculiar Pigmentation of the Silky Fowl. *Journal of Genetics*, I.
 DAVENPORT, C. B. (1906). Inheritance in Poultry. *Carnegie Inst., Wash. Publ.* 53.
 — (1909). Inheritance of Characteristics in Domestic Fowl. *Carnegie Inst., Publ.* 121.
 DAUTHENAY, H. (1905) and Others. *Répertoire de Couleurs*, publié par la Société Française des Chrysanthémistes, Paris, et René Oberthür.
 GOODALE, H. D. (1918). Internal Factors influencing Egg Production in the Rhode Island Red Breed of Domestic Fowl. *American Naturalist*, LII, pp. 65, 209 and 301.
 GOODALE, H. D. AND MACMULLEN, GRACE (1919). The Bearing of Ratios on Theories of the Inheritance of Winter Egg Production. *Journal of Experimental Zoology*, xxviii, April, pp. 83, 124.
 HADLEY, P. B. (1913—1914). Studies on Inheritance in Poultry. *R. I. A. E. S., Bull.* 155 and 161.
 HURST, C. C. (1905). Experiments with Poultry. *Reports to the Evolution Committee of the Royal Society*, Report II, pp. 131—154 (see p. 214).
 — (1907). Mendel's Law of Heredity and its Application to Poultry Breeding. *Report of Second National Poultry Conference at Reading*, pp. 89—96 (see p. 265).
 — (1913). Breeding Experiments with Utility Poultry (V), and On the Inheritance of Minute Variations in Garden Races of Antirrhinum (I). *Reports to Birmingham Meeting of the British Association for the Advancement of Science* (Sections D, K and M.) (See p. 456.)
 LIPPINCOTT, W. A. (1918). The Case of the Blue Andalusian Fowl. *American Naturalist*, LII.
 MORGAN, T. H. (1919). *The Physical Basis of Heredity*. (Lippincott.)
 PEARL, R. (1912). The Mode of Inheritance of Fecundity in the Domestic Fowl. *Journal of Experimental Zoology*, xiii, August, pp. 153—268.
 PEARL, R. AND SURFACE, F. M. (1909). Data on the Inheritance of Fecundity obtained from the Records of Egg Production in the Daughters of "200-egg" Hens. *Maine Agricultural Experiment Station Annual Report*, Bulletin 166, pp. 49—84.
 PUNNETT, R. C. (1919). *Mendelism*. (Macmillan.)
 PUNNETT, R. C. AND BAILEY, P. G. (1920). Genetic Studies in Poultry. II. Inheritance of Egg Colour and Broodiness. *Journal of Genetics*, x, December, pp. 277—292.
 STURTEVANT, A. H. (1913). The Himalayan Rabbit Case, with some Considerations on Multiple Allelomorphs. *American Naturalist*, XLVII.

THE GENETICS OF FECUNDITY IN THE DOMESTIC HEN¹

Six years' experimental breeding and testing on Mendelian lines from 1910 to 1916 gave results which show that the fecundity of a hen depends on the combined action and reaction of many genetic factors.

Seven main genetic factors have so far been identified in the experiments. Five of these, E, W, S, M, and H, influence fecundity, one affects egg-size (N) and one egg-colour (C). Of the five factors influencing fecundity E and W together determine winter production, S is manifested in spring production, M influences autumn production, while H affects the production of any of the three periods.

The seven pairs of Mendelian factors are as follows:

E	e	Early and late sexual maturity of pullets.
W	w	Fast and slow rate of winter production.
S	s	Fast and slow rate of spring production.
M	m	Slow and fast rate of autumn production.
H	h	Broody and non-broody instinct (Hurst, 1905).
N	n	Small and large egg-mode (Hurst, 1913).
C	c	Brown and white egg-mode (Hurst, 1905 and 1913).

The first of each pair is dominant and the second recessive. In order to analyse the complex and continuous data of egg-production a system of uniform gradings was formulated, which ultimately led to the identification of the above genetic factors.

Sexual maturity was measured by age at first egg and graded in months of thirty days.

Early grades (E) were 4 to 8 and late grades (e) 9 to 13, so that each hen had a somatic grading E4 to e13, while each hen and cock had a genetic formula EE, Ee, or ee.

Rate of production was measured by percentage of eggs laid to number of days in lay, for each of the winter, spring, and autumn periods. These percentages were graded in tens.

¹ Communicated to the Second International Congress of Eugenics, New York, Sept. 22—28, 1921, and reprinted from *Eugenics, Genetics and the Family*, I. pp. 212—217 (1923). (Williams and Wilkins, Baltimore.)

Winter period was from first egg to last day of February, spring period from March 1 to June 30 and autumn period from July 1 to last egg of year.

Fast winter grades (W) and fast spring grades (S) were 8 to 3 and slow winter grades (w) and slow spring grades (s) were 2 and 1.

Slow autumn grades (M) were 0 to 2 and fast autumn grades (m) were 3 to 6.

Broodiness was measured by number of broody periods. Broody grades (H) were 6 to 1 and non-broody grade (h) 0.

Egg-size was measured by weight of egg in ten equal grades of 3.5 grams ranging from 42.5 to 74 grams. Small-egg grades were 1 to 4 and large-egg grades 5 to 9. The mode-grade of the first year's eggs was taken to represent the egg-size of each hen.

Egg-colour was measured by grading in six colour shades of equal difference of intensity from dark-brown to chalky white, viz.: dark brown (5), brown (4), light brown (3), cream (2), ivory (1), and white (0). Brown grades 5 to 3 and white grades 2 to 0. The mode of the first year's egg was taken to represent the egg-colour of each hen.

Four breeds were used in the experiments, namely, White Leghorn, White Wyandotte, Light Sussex and Pit Game, including three distinct utility strains of Leghorns and Wyandottes.

In the course of the experiments more than 50,000 eggs were recorded, and each egg was weighed and graded for size and colour.

Four hundred and thirty pullets of four generations were reared from mated pairs, and each pullet was tested for egg-production for one year after first egg where possible.

The unequal influences of the external conditions were minimised by the adoption of certain uniform methods of housing, feeding and exercise which involved the keeping of each individual in a single house or run. (See fig. 165.) The factorial constitutions of 42 sires and 135 dams for the seven genetic factors were determined as far as possible.

The genetic constitutions of the birds were ascertained by a combination of the following four tests: (1) somatic (hens only), (2) parental, (3) progeny qualitative, (4) progeny quantitative. This combination method of analysis was necessary owing to the comparatively small families of pullets raised from the mated pairs and proved to be critical in its complex harmonies.

The following table gives a summary of the results of the experiments with White Leghorns and White Wyandottes on the basis of the scheme of the seven pairs of factors and the genetic analysis involved.

Reduced to terms of dominants and recessives the total numbers are 1195D:687R showing a net deficiency of 17·75 dominants and a corresponding excess of recessives in the total of 1882 observations, or less than 1 per cent.

The gross divergence in the results of the seven factors amounts to 30·25 or less than 2 per cent.

Summary of results in White Wyandottes and White Leghorns.

Characters	Totals	Dominant	Observed	Calculated	Recessive	Observed	Calculated
Sexual Maturity	335	Early (E)	286	289·00	Late (e)	49	46·00
Winter Rate ...	266	Fast (W)	231	231·75	Slow (w)	35	34·25
Spring Rate ...	224	Fast (S)	216	217·25	Slow (s)	8	6·75
Autumn Rate ...	194	Slow (M)	140	145·50	Fast (m)	54	48·50
Broodiness ...	201	Broody (H)	50	58·50	Non-B. (h)	151	142·50
Egg-size ...	331	Small (N)	135	128·75	Large (n)	196	202·25
Egg-colour ...	331	Brown (C)	137	142·00	White (c)	194	189·00
Totals ...	1882	—	1195	1212·75	—	687	669·25

Eighteen definite exceptions appeared of which 2 proved to be somatic and not genetic, 11 were slight exceptions probably of the same nature, 3 were pathological, 1 was possibly an incomplete dominant, while 1 was apparently a true mutation.

Pearl's discovery of two genetic factors for winter production in Plymouth Rocks (1912) confirmed by Goodale and MacMullan in Rhode Island Reds (1918 and 1919) is also confirmed in White Leghorns and White Wyandottes. But as neither Pearl's factors L_1 and L_2 nor Goodale's factors A and B are individually identified with sexual maturity (E) or with rate of production (W), and as Pearl's factor L_2 is sex-linked, while the others are not, it seems impossible to identify factors E and W definitely either with Pearl's L_1 and L_2 , or with Goodale's A and B. No sex-linkage was found either in the White Leghorns or White Wyandottes used in the experiments. In this respect these two breeds agree with Goodale's Rhode Island Reds rather than with Pearl's Plymouth Rocks (cf. p. 508).

No winter zero birds appeared in the White Leghorns, though 9 appeared in the White Wyandottes, and the Wyandotte-Leghorns. All were late maturers (ee) and all the five zeros tested genetically carried the factor W, so that Pearl's interpretation that the zero winter producers in Plymouth Rocks are mostly due to the absence of both production

factors is not borne out in Leghorns or Wyandottes. The Wyandotte zeros on the contrary resemble Goodale's zeros in Rhode Island Reds, their zero production being due entirely to their very late sexual maturity. It is possible, however, that this very late maturity may be due to a genetic sub-factor (cf. p. 483).

In all the factors except H (broodiness) dominance tends to be incomplete, and the heterozygotes are more or less intermediate. In many cases it is possible to recognise the homozygous individuals by their extreme grades, though not always.

In each of the seven main genetic factors for egg-production there are distinct indications of the presence of one or more sub-factors, but the numbers are insufficient to determine these and their allelomorphs satisfactorily. It is possible that an intensive study of a single set of these sub-factors would throw some light on the nature of the "fractional factors" of Bateson (1914) and the "multiple allelomorphs" of Sturtevant (1913) and others.

There appears to be a definite difference of rhythm between the fast (W) and fast (S) birds and particularly between the discontinuous slow (w) and the discontinuous slow (s) birds, and it is not improbable that the slow (s) birds are pathological.

The M factor is clearly of a different nature from the factors W and S, seeing that in the two latter fast rate is dominant, while in the former it is recessive. A striking somatic difference was observed between M and m birds apparently coinciding with their different rates of production. The M birds are deep autumn moulters and slow producers, while the m birds are partial autumn moulters and fast producers. The m mutation, which has incidentally made the "300-egg hen" possible, is interesting genetically on account of its comparatively recent appearance.

Owing to the fact that a sensible proportion of broody hens do not show their broodiness until their second season of laying, it has not been possible to ascertain the true nature of the "non-broodies" in the experiments, as most of them were only observed during their first laying year. Consequently the results show a deficiency of broodies. The appearance of a few broody exceptions in the non-broody Leghorns gives support to Punnett's (1920) suggestion of the possible presence of an inhibitor to the broody factor in certain non-broody birds. The evidence for the HI scheme for broodiness is admittedly incomplete, and experiments on a considerable scale would be necessary to demonstrate it. At the same time it seems to bring into line most of the compli-

cated and conflicting data of the genetics of broodiness that have been published.

Evolutionary significance. The genetic results indicate the gradual evolution of the increase of fecundity in the hen by a succession of definite and discontinuous steps or mutations. Three of these mutations are dominant, viz.: early maturity (E), fast winter rate (W) and fast spring rate (S), while two are recessive, viz.: fast autumn rate (m) and non-broodiness (h). A single case of the solitary appearance of a recessive mutation was observed, in the experiments, which apparently originated in a male Wyandotte by the loss or absence of the factor N (small-egg mode) in a single gametogenesis giving rise to a daughter and grand-daughters with large-egg modes (n). If the original mutation (n) arose in the same way in the wild species, at least two generations would elapse before it could appear owing to its recessive nature, and the lack of a recessive mate. In view of the recent contributions to the chromosome theory of the mechanism of heredity by Morgan (1919) and his colleagues, it is unfortunate that the above experiments do not provide sufficient suitable matings for testing linkages satisfactorily, for investigations in this direction might lead to results of considerable genetic and economic importance.

Economic significance. It is obvious that these genetic results are of considerable economic importance, and the possibilities of their application to practical poultry breeding have been dealt with elsewhere (pp. 511—518).

Eugenic significance. From the problem of fecundity in the domestic hen to the problem of fertility in Man is admittedly a far cry. The cases are by no means parallel though they are in many respects analogous.

Pearl and Surface (1909) rightly distinguish fecundity from fertility, and use the term *fecundity* to "designate the innate potential reproductive capacity of the *individual organism*, as denoted by its ability to form and separate from the body mature germ-cells. Fecundity in the female will depend upon the production of ova, and in the male upon the production of spermatozoa. In mammals it will obviously be very difficult, if not impossible, to get reliable quantitative data regarding pure fecundity. On the other hand we would suggest that the term '*fertility*' be used to designate the total actual reproductive capacity of *pairs of organisms*, male and female, as expressed by their ability when mated together to produce (*i.e.*, to bring to birth) individual offspring. Fertility, according to this view, depends upon and includes fecundity, but also a great number of other factors in addition. Clearly it is

fertility rather than fecundity which is measured in statistics of birth of mammals."

We have seen above that at least five pairs of genetic factors are concerned with fecundity in the domestic hen, and if we accept Pearl's view that fecundity is only a part of fertility, we may expect fertility in fowls to be of a still more complex nature genetically. But the genetic factors of fertility are only a part of the general problem of fertility, for to these must be added the multitudinous somatic or environmental factors, many of which are yet unknown to science.

If the problem of the causes of fertility in poultry is clearly so complex, one can hardly expect the problem of the causes of fertility in Man to be of a more simple nature.

It is evident that there can be no eugenic control of fertility and sterility in Man until the causes of that fertility and sterility are known, and the first line of attack might well be directed to the identification of the genetic factors of human fertility and sterility.

REFERENCES.

- BATESON, W. (1914). *Presidential Address to British Association for the Advancement of Science* (Australia).
- GOODALE, H. D. (1918). Internal Factors influencing Egg Production in the Rhode Island Red Breed of Domestic Fowl. *American Naturalist*, LII, pp. 65, 209 and 301.
- GOODALE, H. D. AND MACMULLEN, GRACE (1919). The Bearing of Ratios on Theories of the Inheritance of Winter Egg Production. *Journal of Experimental Zoology*, XXVIII, April, pp. 83, 124.
- HURST, C. C. (1905). Experiments with Poultry. *Reports to the Evolution Committee of the Royal Society*, Report II. pp. 131—154 (see p. 214).
- (1913). Breeding Experiments with Utility Poultry. *Report V to Birmingham Meeting of the British Association for the Advancement of Science*. (Sections D, K and M.) (See p. 461.)
- MORGAN, T. H. (1919). *The Physical Basis of Heredity*. (Lippincott.)
- PEARL, R. (1912). The Mode of Inheritance of Fecundity in the Domestic Fowl. *Journal of Experimental Zoology*, XIII, August, pp. 153—268.
- PEARL, R. AND SURFACE, F. M. (1909). Data on the Inheritance of Fecundity obtained from the Records of Egg Production in the Daughters of "200-egg" Hens. *Maine Agricultural Experiment Station Annual Report*, Bulletin 166, pp. 49—84.
- PUNNETT, R. C. AND BAILEY, P. G. (1920). Genetic Studies in Poultry. II. Inheritance of Egg Colour and Broodiness. *Journal of Genetics*, x, December, pp. 277—292.
- STURTEVANT, A. H. (1913). The Himalayan Rabbit Case, with some Considerations on Multiple Allelomorphs. *American Naturalist*, XLVII.

XXXVII

ON THE ORIGIN OF THE MOSS-ROSE¹

The old Moss-Rose (*R. muscosa* Mill.) offers genetical problems of considerable interest.

It is identical with the old Cabbage-Rose (*R. centifolia* L.) except in the multiply branching of its gland-bearing structures, *i.e.*, its glands are compound, and not simple as in *R. centifolia* L.

Twelve authors give the Moss-Rose specific rank as *R. muscosa* Mill.; nine regard it as a variety of *R. centifolia* L., while six modern authors place both under *R. gallica* L.

The Cabbage-Rose (*R. centifolia* L.) has been in cultivation in Europe for more than 2000 years, and was probably introduced there from Asia, where it may have been in cultivation from time immemorial, consequently its origin and native country can only be surmised.

It was cultivated by the Greeks and Romans, and is mentioned by Herodotus, Theophrastus and Pliny. The date of its introduction into England is not definitely known, but it is noted and figured by the herbalists of the sixteenth and seventeenth centuries under various names until Linnæus gave it the old name of *R. centifolia*, by which it was known to Theophrastus about 350 B.C.

The Moss-Rose (*R. muscosa* Mill.) is of comparatively recent origin. It does not seem to have been mentioned by the ancients, nor by the older herbalists, and a careful search reveals no evidence in support of the repeated statements in English horticultural literature from 1843 to 1920 that the Moss-Rose was introduced from Holland in 1596.

The earliest date mentioned of the existence of the Moss-Rose appears to be the year 1696, when it was said to be in cultivation at Carcassonne in France, on the authority of Fréard Ducastel (1746), who introduced it to three districts in the west of France.

The first botanical reference to the Moss-Rose is apparently that of Boerhåave in his *Index of Plants cultivated at Leyden* in 1720, which is confirmed by Miller who states in 1760 that he first saw it there in 1727, and brought a plant to England.

¹ Read before Section K of the British Association for the Advancement of Science, Edinburgh Meeting, Sept. 1921.

Curiously enough in Miller's original edition of his *Dictionary* dated 1724 it is included in a list of plants cultivated at Kensington by Robert Furber, though it is not mentioned in Miller's text.

It was figured in Furber's large folio *Catalogue of Plants* in 1730, and a specimen was deposited by Miller in the British Museum in 1735.

Darwin quotes Shailer's (1852) account that the Moss-Rose was imported from Italy about 1735. Darwin's conclusion that the original Moss-Rose was probably a bud-variation of *R. centifolia* is fully confirmed by additional facts brought to light in this inquiry.

Incidentally 63 bud-variations of *R. centifolia* L. have been traced through several bud generations, and to distinguish the successive generations of bud-variations the notation B_1 , B_2 , B_3 , and so on, is suggested on similar lines to the familiar Mendelian notation of F_1 , F_2 , F_3 , introduced by Bateson in 1902 for seed-variations.

The bud-variations found in the Moss-Rose in B_2 are precisely parallel to those found in the Cabbage-Rose in B_1 , owing no doubt to their similar genetic constitution and common origin. The sole difference being in the presence or absence of the "Moss" character.

Since the first appearance of the "Moss" mutation in B_1 about 1696, two similar mutations have appeared in B_2 of *R. centifolia* L., viz., the Moss de Meaux in 1801 in England as a bud-variation of the Dwarf Cabbage-Rose de Meaux, and the Unique Moss in France about 1843 as a bud-variation of the White Cabbage-Rose Unique.

No other "Moss" mutation appears to have been recorded in *R. centifolia* L. or in any other species of *Rosa*, and all other Moss-Roses have apparently been derived directly from Moss-Roses.

Up to the year 1807 the five varieties of the Moss-Rose that had appeared were all due to bud-variations, for naturally and normally the flowers are infertile as in the bud-parent *R. centifolia* L.

No records of the production of fertile seeds by either the typical *R. centifolia* L. or *R. muscosa* Mill. can be traced in botanical or horticultural literature. No fully formed and mature fruits have been observed on either form at Burbage under normal conditions, during the last seventy years, though partly formed fruits containing no seeds have been frequently found.

The precise nature of this infertility has not yet been made out, but from the evidence so far obtained it would appear that it may be due to some extent to the involuted multiplication of the petals of the flower peculiar to both the typical *R. centifolia* L. and *R. muscosa* Mill., whose tightly-balled petals and petaloid stamens seem to inhibit the

natural development of the pistils. To test this, a number of flowers were artificially operated on this summer; at an early stage the petals, petaloid stamens and stamens were carefully removed and the pistils released and allowed to develop freely, with the result that, for the first time, 15 apparently good fruits have been obtained (12 selfings and 3 crossings); one of the selfed fruits was opened and found to contain a single normal seed.

It is possible, however, that the abnormal sunshine experienced this summer contributed to this success, and too much stress must not be laid on it, for notwithstanding the favourable conditions, there were many failures, and on the whole *R. centifolia* L. and *R. muscosa* Mill. must still be regarded as sterile in the Darwinian sense, *i.e.*, not fully fertile.

With regard to the question of the fertility of the pollen in typical *R. centifolia* L. and *R. muscosa* Mill. an examination of many flowers shows that about 90 per cent. of the stamens have been changed into petals or petaloid stamens, leaving in each flower from 6 to 12 anthers containing pollen-grains.

A microscopical examination of the pollen-grains shows about 95 per cent. of malformed grains in both forms, the chief difference being the presence in *R. muscosa* Mill. of a number of abnormally large grains showing signs of hypertrophy, and in both forms degeneration of pollen was found even in the early tetrad stage.

This result contrasts remarkably with the 99 per cent. of well-formed grains found in *R. rugosa* Thunb. and *R. arvensis* Huds. in all stages of development, but resembles rather the large percentage of malformed grains found in *R. wichuraiana* Crép. and *R. laxa* Hort. at all stages, while the closed buds of the former also contained a large number of what appear to be hypertrophied grains.

Attempts to germinate the few apparently good pollen-grains of *R. centifolia* L. and *R. muscosa* Mill. have so far failed both on the natural stigmas of the fertile *R. rugosa* Thunb. and in sugar solution. On the other hand under the same conditions the many good grains of *R. rugosa* Thunb. germinated freely and normally, while some of the few apparently good grains of *R. wichuraiana* Crép. germinated abnormally and unsatisfactorily.

Several stigmas of selfed flowers of *R. laxa* Hort. were examined and only one pollen-grain was found that showed signs of germination.

For these interesting microscopical results I am indebted to the careful and assiduous work of Miss M. S. G. Breeze, B.Sc., of the School of Agriculture, Cambridge.

It is interesting to note that Miss Breeze, who has been for some time investigating the nature of defective pollen in *Solanum*, *Petunia*, etc., finds in the *Rosa* pollen she has examined for me, the similar association of large numbers of bacteria and other minute organisms with defective pollen-grains, that she found in Potato pollen. The fact that these organisms are found in all the stages from the pollen mother-cell and tetrad stage in very young and tight flower-buds onwards and with the defective pollen only, is certainly remarkable and may prove to be of significance. Täckholm (1920) and Blackburn and Harrison (1921) have presented some remarkable cytological results in *Rosa* and agree in concluding that the large amount of abortive pollen found in the *Canine* Section is immediately caused by the irregular distribution of the unpaired chromosomes in the reduction divisions.

Both authors ascribe this irregular behaviour of the chromosomes to hybridity, and Täckholm claims that a cytological examination will demonstrate whether a hybrid belongs to the F_1 or F_2 (or later) generation.

It is possible that *R. centifolia* L. (with defective pollen) may be an ancient hybrid, for in many of its characters it resembles both *R. gallica* L. and *R. moschata* Herm. It is more difficult, however, to recognise *R. wichuraiana* Crép. (with defective pollen) as a hybrid, and though it has certain resemblances to *R. multiflora* Thunb. and *R. bracteata* Wendl. (both natives of China), its peculiar trailing habit of growth is very distinct from either.

As a practical test of fertility a number of pollinations were made this summer on various fertile species and hybrids of *Rosa* with the defective pollen of *R. centifolia* L. and *R. muscosa* Mill. with the result that 29 fruits have been produced (12 selfings and 17 crossings) which may or may not produce good seeds.

In consequence, however, of the apparent prevalence of apomixis in the genus *Rosa*, even if good seeds are produced in these fruits, some time must elapse before it can be stated definitely whether these pollinations have resulted in fertilisations or not.

Recent results at Burbage show that all the polymorphic local forms of the *Canine* Section of *Rosa* (including *R. laxa* Hort.) so far tested (16 forms) are apparently facultatively apomictical when planted side by side and seeded naturally with uncovered flowers, thus confirming to some extent Täckholm's (1920) conclusion that they may represent ancient F_1 hybrids that have maintained themselves by apomictical reproduction possibly for thousands of years.

There are also many indications this year of facultative apomixis in other sections of the genus, especially in the selfed garden hybrids of *R. indica* Lindl., *R. damascena* Blackw. and *R. lutea* Mill.

In this respect Täckholm's (1920) assumption that the tetraploid Roses showing all the chromosomes in paired condition in diakinesis have exclusively sexual reproduction, is not confirmed.

This summer, flowers of *R. laxa* Hort., *R. andegavensis* Bast., and others, have produced normal fruits and seeds notwithstanding the entire removal of the stamens and stigmas at an early stage. These results appear to demonstrate apomixis and explain why seedlings of *R. laxa* Hort. normally breed so true to the mother plant, notwithstanding its possible hybrid origin.

Such facts also go far to explain the absence of Mendelian segregation in the selfed seedlings of many species-hybrids, and show how hybrids can breed true.

The question as to whether apomixis in *Rosa* is simple parthenogenesis, apogamy, apospory, polyembryony or some other form of maternal reproduction, is a difficult one, but it is hoped that it will be possible to determine this interesting point in the near future.

The *R. laxa* Hort. referred to in these experiments is used largely in Nurseries as a stock for garden Roses, but its precise botanical position does not appear to have been ascertained.

It clearly belongs to the *Canine* Section of the genus (in the broad sense) and is quite distinct from *R. laxa* Retz. and *R. laxa* Lindl. both of which belong to the *Cinnamomeae* Section. It is closely allied to *R. alba* L., *R. dumetorum* Thuill., *R. Deseglesii* Bess. and *R. venosa* Swartz. and is possibly of hybrid origin. *R. laxa* Hort. has been in cultivation at Burbage since 1905 and was first obtained from a nursery in Normandy.

(Since the above was written, I note that Dr Galloway of the U.S.A. Department of Agriculture (1920) refers *R. laxa* Hort. to *R. coriifolia* var. *Fräbelii*, but as Dr Heslop Harrison points out, after a comparison of my material with his northern forms of *R. coriifolia* Fries, the characteristic broad, flat, woolly head of stigmas, that distinguishes *R. coriifolia* Fries, is absent in *R. laxa* Hort.)

To return to the question of the normal infertility of *R. muscosa* Mill., in 1807 a single-flowered bud-variation appeared on the Old Moss-Rose with Shailer of Chelsea; this proved to be fertile and was the original ancestor of numerous garden hybrids including the many modern Moss-Roses raised in France and England between 1824 and 1860.

The fact that bud-variation is common in the infertile *R. centifolia* L. and rare in the fertile related species *R. gallica* L. and *R. damascena* Mill. suggests that there may be a definite connection between infertility and bud-variation in this group, and it seems not unlikely that the phenomenon of bud-variation may be regarded as an alternative mode of expression of variation in the absence of fertility.

The sterility of the Old Moss-Rose raises a distinct difficulty in the investigation of the genetics of the "Moss" mutation, especially as the Single Moss of 1807 seems to be no longer in cultivation, though as we have seen this difficulty is probably not insurmountable.

From the results obtained by Rivers and others with the Single Moss all the evidence is in favour of the "Moss" factor being a simple dominant. And as the Old Moss-Rose has on at least ten occasions between 1805 and 1873 produced bud-reversions to the old Cabbage-Rose, and the Single Moss gave "plain" Roses, as well as "Moss" Roses when crossed with "plain" Roses, it is probable that the Old Moss-Rose is a heterozygous dominant.

In terms of the recent developments of the chromosome theory of heredity it may be said that the "Moss" mutation arose through the presence of an additional factor in a single locus of a single chromosome of a somatic cell.

If that is so, bud-mutations take on a new importance and the case of the Moss-Rose is of considerable significance, for it promises to provide simple material for attacking afresh the problem of the origin of a mutation.

XXXVIII

CHROMOSOMES AND CHARACTERS IN *ROSA* AND THEIR SIGNIFICANCE IN THE ORIGIN OF SPECIES¹

The genus *Rosa* is admittedly a difficult one in many ways. It has defied the efforts of many systematists since the time of Linnæus (1753) who remarks in *Species Plantarum* that the species of *Rosa* are very difficult to determine, and he adds naively that those who have seen few species can distinguish them more easily than those who have examined many. In spite of the strenuous and life-long labours of Lindley, Christ, Crépín, Baker, Almquist and others, it must be admitted that no entirely satisfactory classification of the multitudinous forms of the genus has been made.

GENETICS OF *ROSA*.

Genetically the genus is almost unknown, and the technical difficulties of raising several generations are very great. My own experiments begun at Burbage 15 years ago are still in their infancy, as the normal time for a generation in many species is about 6—8 years, and 6 years were lost owing to the War. The genetical slowness of *Rosa* material is however fully compensated by its permanence, for the individual plant is able to live to an extreme age, and its life can be indefinitely prolonged by vegetative propagation.

CYTOLOGY OF *ROSA*.

Cytologically an extended knowledge of the genus dates only from 1920 when Täckholm (1920), (1922), and Blackburn and Harrison (1921), almost simultaneously showed that the fundamental number of chromosomes in *Rosa* is 7, and not 8 as previously stated by Strasburger (1904), (1910).

Thanks to the facilities granted by the University Authorities at Cambridge it has been possible for me to work out the chromosome complexes of a number of unexamined forms of *Rosa* from material collected at Cambridge, Kew, Paris and my genetic material at Burbage. The

¹ Abstract of papers read at the British Association at Liverpool September 14th, 1923, and before the Genetical Society, London, December 8th, 1923.

results fully confirm the findings of Täckholm (1920), (1922), and Blackburn and Harrison (1921), that the fundamental number of chromosomes in *Rosa* is 7.

SEPTUPLE CHROMOSOME NUMBERS.

Further the results show that all the somatic and gametic chromosomes examined are either 7 or a multiple of 7. Somatic chromosomes are diploid 14, triploid 21, tetraploid 28, pentaploid 35, hexaploid 42, or octoploid 56. (Fig. 169 *a—f*.)

Täckholm (1922) reports 4 cases of aneuploid *Rosæ* out of 293 examined, which he presumes are F_2 or F_3 hybrids, and it is possible that cases of aneuploidy may occur in *Rosa* species though, so far, I have not been able to find one.

Gametic chromosomes, male and female, are either *equal* with 7—14—21 or 28 each, or *unequal and matroclinous* with a maternal bias in the ratio of 1·5—2—3—4 or 5:1. All are 7 or a multiple of 7, for if they were not, aneuploids would be frequent (fig. 169 *g—l*).

SEPTETS OF CHROMOSOMES.

So far all the somatic and gametic chromosomes of *Rosa* appear to be equal in size and alike in form in both diploid and polyploid species. In the polyploid species however the nuclei are correspondingly larger as the number of chromosomes increases.

The significance of the septuple numbers of chromosomes in *Rosa* is apparent in various stages of gametogenesis and also in some somatic divisions in diploids and polyploids, in which it is evident that the chromosomes are working in sets of seven or septets. (Figs. 170—172.)

SIGNIFICANCE OF THE SEPTETS.

At the time no special significance was attached to the septets beyond that it confirmed previous observations that in *Rosa* the chromosomes were working in sevens. Like others one regarded tetraploidy and polyploidy as simply a duplication and reduplication of the chromosomes of the diploid species such as one finds in *Oenothera* (Gates (1915)), *Primula* (Gregory (1914), Farmer and Digby (1914)), *Datura* (Blakeslee (1920)), and which the author has also found in several cultivated forms of *Rosa*. One looked upon the septets of chromosomes in the spontaneous species of *Rosa* as sets of seven chromosomes which had in some way been duplicated and reduplicated. But one day when comparing the taxonomic characters of the species in the living collection at Kew, one was struck by the fact that the tetraploid species showed the combined

characters of two distinct diploid species, while the hexaploid species showed the combined characters of three distinct diploid species and the octoploid species showed the combined characters of four distinct diploid species.

FIVE DIFFERENTIAL DIPLOID SPECIES.

These observations suggested that the four double septets in the octoploid species were not simple reduplications of the double septet of a single diploid species, but, on the contrary represented the four differential septets of four distinct diploid species in combination.

Taxonomic analyses of the 200 forms of *Rosa*¹ examined cytologically by Täckholm (1922) and myself, from material collected at Kew, Paris, Cambridge and Burbage, fully confirmed the previous observations, except that the characters in the polyploid species were found to be represented in five differential diploid species instead of four, which number (five) corresponds with the five septets of chromosomes found in *Rosa*. So far a decaploid species with five double septets of chromosomes has not been discovered, but four irregular hexaploid forms with five differential septets of chromosomes and characters are in existence (*R. Jundzilli* Bess., *R. glutinosa leioclada* Christ, *R. stylosa evanida* Christ and *R. inodora* Fries), and it is not at all unlikely that the missing decaploid species may soon be identified.

Whether the missing decaploid be found or not is, however, immaterial since the four forms above clearly demonstrate that five distinct septets of chromosomes and characters may be present in *Rosa*. That these five septets are distinct from one another is clear since the above forms show the characters of five distinct diploid species.

The five differential septets of chromosomes in *Rosa* may therefore be distinguished as A—B—C—D and E and the double septets in each differential diploid species as AA—BB—CC—DD and EE.

In view of the remarkable results achieved by Morgan and his colleagues in *Drosophila*, we may now safely presume that the A septet of chromosomes carries the factors which determine the A set of characters in the AA diploid species, and so on with the B—C—D and E septets of chromosomes in the BB—CC—DD and EE diploid species.

Since the five diploid species AA—BB—CC—DD and EE carry only one *distinct* (double) septet each, they may be distinguished as the five differential septet species of *Rosa*.

So far about 50 different taxonomic characters have been recognised

¹ Since extended to 400 forms. (Note added 1924.)

in each of the five differential septet species (fig. 173). Each set of septet characters is distinct from the other four sets and no corresponding septet characters are precisely alike. An analysis of the septet characters shows that while some of them are constant, others are variable and alternative, which leads one to suppose that the constant characters are homozygous while the alternative characters are segregates of heterozygous forms within each septet. This explains the great variability that is found within the five differential septet species, while the general facies remains the same. Some systematists make as many as 40 species out of the five, largely on the ground of their geographical distribution and isolation, but the evidence collected shows that these 40 forms are more reasonably interpreted as geographical sub-species.

It is evident from these and other considerations that the five differential diploid species of *Rosa* are real discontinuous species, with no intergrading or transitional forms, since each has its own set of at least 50 taxonomic characters which are distinct from the other four sets of characters. Each has a septet of chromosomes which is double in the somatic cells and single in the gametes and presumably the five differential sets of taxonomic characters are represented in the five corresponding differential septets of chromosomes.

DIFFERENTIAL SEPTET CHARACTERS IN POLYPLOID SPECIES.

The polyploid species of *Rosa*, so far known, are triploid, tetraploid, pentaploid, hexaploid or octoploid in their septets of chromosomes.

Certain cultivated triploid and tetraploid forms are obviously duplicated forms which have arisen in various ways under cultivation by duplications of the septets of chromosomes in the original diploid species. These naturally maintain the specific characters of the original diploid species while displaying the various varietal segregations peculiar to the species. In certain cases, *e.g.* the tetraploid form *R. odorata* Swt. var. *Gloire de Dijon*, whose septet formula is AAAA, certain peculiarities of structure (*e.g.* giantism) are present in the duplicated forms which possibly may be due to the chromosomes having been duplicated by longitudinal splitting as in *Ænothera gigas* (Gates 1915) rather than by latitudinal fragmentation as in *Primula kewensis* (Digby 1912 and Farmer and Digby 1914).

On the other hand the spontaneous polyploid species of *Rosa* examined are clearly not duplicated diploids but differential polyploids, with differential septets of chromosomes since they show in their taxonomic characters various combinations of the differential septet characters of the

five differential diploid species. For instance the tetraploid sub-species *R. gallica* L. has the septet formula AACC, the pentaploid *R. canina* L. var. AABDE, the hexaploid *R. Moyesii* Hemsl. and Wils. AABBE and the octoploid *R. acicularis* Lindl. BBCCDDEE.

The various combinations of the characters of the five differential diploid species AA—EE give the 206 compound septet species in the spontaneous differential polyploids.

The manner of working of the septet factors in the differential polyploid species has not yet been fully ascertained, but there is sufficient evidence to show that as a rule each septet works equally with but independently of the other septets with which it may be associated. So far no cases of blending nor of the general dominance of one septet over another have been found.

In the pentaploid species however, where there is one double septet working with three single septets as in AABDE species (*R. canina* L. var.), the double A septet seems to be working in twice as many characters as in any of the single B, D or E septets.

In the most complex case studied, in the octoploid species BBCCDDEE (*R. acicularis* Lindl.), the four double septets seem to work more or less in relays in different parts of the plant at different times and seasons, resulting in a periodic predominance of one septet over another in certain parts of the plant, the general result being more or less a mosaic of the four septets of characters arranged end to end or side by side.

Naturally with four double septets working equally and independently in an octoploid species, only about one-fourth of the characters of each septet can be represented at one time. An analysis shows that in a plant of *R. acicularis* Lindl. carrying four years' growth of surculi, stems, branches and branchlets, about one-half of the characters of each of the four septets B, C, D and E were represented (fig. 174 *e* and *f*).

An interesting case was observed in the author's experiments in which several plants of the tetraploid species AACC (sub-sp. *R. centifolia* L.) grown in a greenhouse for a genetical experiment, developed *temporarily in the second season* the climbing character of the sub-tropical A septet, a feature usually absent when grown under natural conditions.

NEW SYSTEM OF CLASSIFICATION OF SPECIES.

The septet characters in *Rosa* provide a natural and precise method of classification of the species of the genus. This classification is based on cytological, genetical, and taxonomic characters combined.

On this basis the genus *Rosa* may be divided into nine sections

according to the numbers of somatic septets of chromosomes present in the species.

The nine sections may be sub-divided into 15 sub-sections according to the numbers of gametic septets present in the species.

The 15 sub-sections may be sub-divided into the 211 simple and compound septet species, according to the possible combinations of the five differential septets of chromosomes and characters. So that the presence or absence of any one of the five septets of chromosomes and characters—double or single—determines the septet species.

This gives a definite and uniform classification of the species of *Rosa*, in which each species in a section or sub-section differs from another simply in a septet of chromosomes and characters. This is probably as close an approximation to a mathematical species as one can hope to get in living organisms.

Workers in genetics and cytology may find such a system of classification useful in other plants and animals, as I have done in *Rosa*, since according to it a species is no longer a question of opinion, but a definite entity that can be precisely determined by a count of the chromosomes and a reference to the table of septet characters.

A large number of Linnean species correspond and coincide with the septet species, and there are considerable numbers of doubtful species and forms in *Rosa* whose positions can be ascertained precisely by the septet system of classification outlined above. For instance, the various forms of *R. tomentosa* Sm. can be distinguished from those of *R. mollis* Sm. by the presence of an additional septet of chromosomes and characters in the former which is absent in the latter, so that *R. tomentosa* has five septets of chromosomes, while *R. mollis* has only four septets. Each septet species, simple or compound, diploid or polyploid, naturally has its own sub-species, varieties and forms which may be indicated if necessary by the addition of indices to the septet formulæ.

ECOLOGICAL DISTRIBUTION.

The most marked feature of the five simple septet species is the striking dissimilarity in their general facies.

A gardener with an experienced eye for the habit of a plant would recognise their distinctness at a glance without reference to their taxonomic characters.

Thus, the tender climbing AA septet species is obviously fitted for temperate and luxuriant conditions of life. The spiny small-leaved

BB septet species is fitted for extremes of drought and heat. The prickly suffruticose CC septet species is fitted for extremes of drought and cold. The reedy stoloniferous DD septet species to extremes of cold and moisture. The cany long-noded EE septet species to extremes of heat and moisture.

From the evidence that I have been able to collect concerning the habitats of the five simple septet species it would appear that each is fitted for a certain habitat. Thus the A septet species is strictly confined to temperate and sub-tropical regions, and is usually found in sheltered places. The B septet species is found in dry, sandy and desert places, with extremes of heat. The C septet species grows in dry rocky places often near the sea, with extremes of cold. The D septet species grows for the most part in cold swamps and marshy ground. The E septet species grows in conditions of heavy rainfall and great heat; under cultivation in England, it is tender and susceptible to drought.

A study of the habitats of these species brings one to the geographical distribution of the species of *Rosa* which is of peculiar interest.

GEOGRAPHICAL DISTRIBUTION.

The evidence shows that on the whole the five simple septet diploid species have a definite southerly bias, while the compound septet polyploid species have a distinct northerly bias. In fact a general statement might be made that towards the Pole the number of septets of chromosomes and characters increases, while towards the Equator the number decreases (fig. 175). Thus all the octoploid species with four double septets of chromosomes and characters are, so far as known, circum-polar, and do not extend far below the Arctic Circle except at high altitudes. The hexaploid species with three double septets of chromosomes and characters are found further south, and where they extend far are usually at high altitudes. The tetraploid species with two double septets of chromosomes and characters occupy on the whole a middle position, though those with "cold" septets often extend northwards, and those with "warm" septets often extend southwards.

The five simple septet diploid species are for the most part found in southerly or temperate regions, the AA septet species extending to the sub-tropics and even to the tropics at high altitudes. As a rule the "warm" BB septet species is not found north of China and California, nor the "warm" EE septet species north of Central China and California, while the "cold" CC septet species extends to North Japan and Newfoundland, and the "cold" DD septet species to Sweden and South Canada.

The fact that the polyploid species of *Rosa* with several differential

septets of chromosomes and characters are found only in northern latitudes, suggests that their several differential septets may be useful to them in the extreme conditions of life in which they grow and reproduce themselves. In such conditions it might be useful for a species to be able to respond at different times and in divers ways to great extremes of cold and heat, moisture and drought, and darkness and light, so that a polyploid species with several differential septets of chromosomes and characters would be more likely to survive and reproduce itself in Arctic conditions than a simple diploid species with only one septet of characters.

EVOLUTION AND ORIGIN OF SPECIES.

This remarkable distribution of the species of *Rosa* leads one to consider the question of their evolution and origin.

The facts of distribution at once suggest two distinct possibilities concerning their evolution: either a line of *descent* from one primitive decaploid species by successive losses of septets of chromosomes and characters, or a line of *ascent* from the five simple diploid species by hybridisation and subsequent duplications of septets of chromosomes and characters. The fact that the polyploid species show the combined characters of the five diploid species seems to support the idea of origin by hybridisation and duplication. On the other hand such a view presents serious cytological and geographical difficulties.

The cytological difficulty is that two diploid species AA and BB hybridised will not give a tetraploid species AABB in F_1 but only a sterile diploid hybrid AB. This hybrid might be fertile by the segregation of whole septets A and B in the male and female reduction divisions, when it would give either sterile diploid hybrids AB like itself, or fertile diploid species AA and BB like its parents. Apparently the only practical possibility of this sterile diploid hybrid AB producing a fertile tetraploid species AABB would be by a duplication of its somatic chromosomes, giving rise to a bud-mutation, which, by self-fertilisation, would reproduce its kind. This, however, would give a homozygous tetraploid species, while all the tetraploid species of *Rosa* are certainly heterozygous. The possibility of a simultaneous duplication of the chromosomes in the uniting male and female gametes is too remote to be seriously considered. In view of the many repeated duplications of this kind necessary to make the ten tetraploid species and the more numerous polyploid species, the probability of origin by hybridisation on the whole seems to be extremely small, though not altogether excluded. The geographical difficulty of the origin of the

polyploid species by hybridisation is that the diploid species necessary to form the tetraploid species are not there to be hybridised. All the five diploid species are widely spread, highly specialised, occupy distinct habitats and usually flower at different times, so that the probability of their being hybridised in the precise pairs necessary to form the ten tetraploid species and the more numerous polyploid species, seems to be very remote. Even if an AB diploid hybrid did happen to arise in an AA habitat, and succeeded in making itself fertile by duplicating its chromosome septets to a tetraploid species AABB, it is exceedingly doubtful whether it would survive and reproduce itself in the AA habitat long enough to be able to migrate into the AABB habitat farther north or at a much higher altitude.

Further, an evolution of the Arctic polyploid species by hybridisation of sub-tropical diploid species would seem to involve a complete reversal of the generally accepted views of the Arctic origin of the flora of the Northern Hemisphere.

Finally, an origin from five primitive diploid species implies a multiple origin with its consequent ulterior problems, while an origin from one primitive polyploid species is a more simple proposition.

On the whole it seems more easy to suppose that a northern decaploid was the primitive species from which the existing species of *Rosa* have descended, by successive losses of septets of chromosomes and characters, thus automatically fitting the lower polyploid species and the simple diploid species for their peculiar habitats.

As the conditions of life became less extreme the necessity of the several septets might become less, and by successive losses of septets the decaploid species would give rise to an octoploid species, the octoploid to a hexaploid species, the hexaploid to a tetraploid species until finally the simple diploid species would emerge better fitted for the more temperate and specialised conditions of life in the South. Further it is probable that the conditions of life themselves may have been the direct cause of these speciations in *Rosa*, for my cytological observations show that a whole septet of chromosomes may be lost, if retarded and left behind in a cell-division, in the species AACC (sub-sp. *R. damascena* L.) that has been subject to changed conditions of life for a considerable period of time¹ (fig. 170 j). (See also fig. 171.)

¹ It is significant that a form of this tetraploid species AACC has produced several triploid forms AAC under cultivation in Holland and France, and it may be significant that the individual form examined by me is said to have been introduced from Persia, where the closely allied pentaploid species AACCE was found growing on Omar Khayyam's grave.

If, owing to changed conditions of life, the working of a certain septet of chromosomes in a polyploid species was not necessary to the life of the plant, by constant disuse it might weaken, lag behind in a cell-division and be ultimately lost. In such cases new species would arise with a septet of chromosomes and characters less than their parents, and these new species would automatically be better fitted to survive and reproduce themselves in the changed conditions of life.

IRREGULAR POLYPLOID SPECIES.

With regard to the origin of the irregular polyploid species of *Rosa* peculiar to Europe and Western Asia, which consist of tetraploid, pentaploid and hexaploid species with some single septets of chromosomes (instead of all double septets as in the regular polyploid species of Europe, Asia, and America), Täckholm (1920) (1922) and Blackburn and Harrison (1921) agree in concluding that all have originated by hybridisation. It must be admitted that both the cytological evidence and the septet formulæ of these species agree with the hybridisation hypothesis. The chief difficulty however in accepting this explanation of the origin of these irregular species is their geographical and ecological distribution, for the necessary parents are seldom there to be hybridised.

Täckholm (1922) explains this by presuming a suitable distribution of the necessary parent species before the Ice Age, but so far as I can ascertain, there is no evidence of this in the palæontological records. On the whole it seems more probable that the irregular polyploid species of Europe and Western Asia have originated in the same way as the regular polyploid species of Europe, Asia and America by losses of septets of chromosomes, the only difference being that while the regular species have lost a double septet at a time, the irregular species have lost only a single septet of chromosomes and characters. At the same time one must admit the probability that some of the irregular polyploid species, particularly those whose putative parents grow in close proximity, have arisen by hybridisation, while others have arisen from somatic or gametic speciations.

CONCLUSION.

In conclusion it may be useful to point out the value of the septet scheme of chromosomes and characters in *Rosa* as a working hypothesis. First, it has already cleared up many of the difficulties pointed out by Linnæus, Lindley, Christ, Crépin, Täckholm and Harrison in their

studies of the genus, and thus enables one to deal with certain problems of classification and origin which before seemed impossible to solve.

It provides a satisfactory explanation of the extraordinary polymorphism in *Rosa* and goes far to explain the chief causes of fertility and sterility in species and hybrids.

It demonstrates the existence of two distinct forms of polyploidy, Duplicated and Differential.

It gives one a new conception of heredity in the differential polyploid species leading to broader conceptions of mutation, evolution and origin of species. Thus it shows that the ordinary Mendelian ratios may only be expected in crosses within a diploid species and consequently explains how non-Mendelian ratios may be expected in crosses within a polyploid species.

It provides a new system of classification of species, based on cytological, genetical and taxonomic characters combined, which not only gives one a precise and uniform definition of a species in what is probably the most polymorphic genus of plants and animals, but has the distinct advantage that each species can be verified experimentally by both cytological and genetical methods.

The septet of chromosomes provides a simple yet vital mechanism for the evolution of the Linnean species of *Rosa*, demonstrating that variations may be large, discontinuous, truly specific and adaptive in the polyploid species (*i.e.* Speciation), while in the diploid species variations will be comparatively small, sub-specific, varietal and Mendelian (*i.e.* Mutation).

The septet scheme of speciation by phylogenetic descent from a primitive polyploid species goes far to explain the geographical distribution of the existing species of *Rosa* in the Northern Hemisphere, and illustrates the point of view that the evolution of species may lead to simplification and specialisation rather than to complexity and co-operation.

Further, it suggests that the existing species of *Rosa* were largely predetermined in the primitive polyploid species and that their evolution has been more or less automatic in response to the conditions of life which have directly caused and controlled the speciations through the losses of the differential septets of chromosomes by disuse, and in this way the changing conditions of life have determined the trend of the evolution of the species throughout the Northern Hemisphere.

Finally, the septet scheme of chromosomes and characters in *Rosa* can be verified experimentally by both cytological and genetical methods, and the following seven crucial experimental tests should be decisive.

EXPERIMENTAL TESTS OF THE SEPTET SCHEME OF CHROMOSOMES
AND CHARACTERS IN *Rosa*.

(1) *Cytological Test*. In any species of *Rosa*, the chromosome number should be found to coincide with the septet formula of the taxonomic characters.

(2) *Genetical Tests*. All crosses between sub-species or varieties of the same diploid species should breed true to the septet characters of that species and their somatic chromosomes should be diploid (14).

(3) All hybrids between diploid species with different septets should have the septet characters of the corresponding tetraploid species, but their chromosomes should be diploid (14).

(4) All hybrids between regular tetraploid species with different septets should have the septet characters of the corresponding octoploid species, but their chromosomes should be tetraploid (28).

(5) All hybrids between regular tetraploid and diploid species with different septets should have the septet characters of the corresponding hexaploid species, but their chromosomes should be triploid (21).

(6) All hybrids between regular hexaploid and tetraploid species with different septets should have the septet characters of the decaploid species, but their chromosomes should be pentaploid (35).

(7) All hybrids between regular octoploid and diploid species with different septets should have the septet characters of the decaploid species, but their chromosomes should be pentaploid (35).

(The cytological test (1) is obviously more rapid than the genetical tests (2)—(7), and has already been carried out successfully many times. The genetical tests have been put in hand, but naturally some time must elapse before they can be completed.)

NOTE ADDED 1925.

Full details of the working of the septet scheme of chromosomes and characters in *Rosa* with numerous photographs, specific tables and maps of distribution already prepared, will be published in the form of a monograph of the genus in several volumes.

Vol. I dealing with "The Five Diploid Species of *Rosa*" will be issued as soon as possible.

Owing to the considerable time that must elapse before the whole of the detailed evidence can be presented, the above "Summary of Conclusions" has been published in the hope that workers in other genera may be able to test how far the *Rosa* principles apply to other plants and animals.

LIST OF AUTHORS.

- BLACKBURN, K. B., AND HARRISON, J. W. H. (1921). The Status of British Rose forms as determined by their cytological behaviour. *Annals of Botany*, xxxv. pp. 159—188.
- BLAKESLEE, A. F., BELLING, J., AND FARNHAM, M. E. (1920). Chromosomal Duplication and Mendelian Phenomena in *Datura* mutants. *Science*, N.S. 52, pp. 388—390.
- DIGBY, L. (1912). The Cytology of *Primula kewensis* and of other Related *Primula* Hybrids. *Annals of Botany*, xxvi. pp. 357—388, pls. 41—44.
- FARMER, J. B., AND DIGBY, L. (1914). On Dimensions of Chromosomes considered in Relation to Phylogeny. *Phil. Trans. Roy. Soc. B.* 205, pp. 1—25, pls. 2.
- GATES, R. R. (1915). *The Mutation Factor in Evolution*. Macmillan, London.
- (1924). Polyploidy. *Brit. Journ. Exptl. Biol.* i. pp. 153—182.
- GREGORY, R. P. (1914). The Genetics of Tetraploid Plants in *Primula sinensis*. *Proc. Roy. Soc. B.* 87, pp. 484—492.
- HARRISON, J. W. H. (1920). The genus *Rosa*, its hybridology and other Genetical Problems. *Trans. Nat. Hist. Soc.*, Northumberland and Durham, N.S., vol. 5, pp. 244—298.
- LINNÆUS, C. (1753). *Species Plantarum*, i. p. 492.
- MORGAN, T. H. (1919). *The Physical Basis of Heredity*. Lippincott, Philadelphia. 305 pp.
- and others (1915). *The Mechanism of Mendelian Heredity*. Holt, New York. 262 pp.
- STRASBURGER, E. (1904). Die Apogamie der Eualchemillen und allgemeine Gesichtspunkte, die sich aus ihr ergeben. *Pringsh. Jahrbuch. für wissenschaft. Bot.* Bd. xli. pp. 88—164.
- (1910). Chromosomenzahl. *Flora*. Bd. 100, pp. 398—446.
- TÄCKHOLM, G. (1920). On the Cytology of the Genus *Rosa*. *Svensk Botanisk Tidskrift*, Bd. 14, pp. 300—311.
- (1922). Zytologische Studien über die Gattung *Rosa*. *Acta Horti Bergiani*, Bd. 7, No. 3, pp. 97—381.

FIG. 169. SOMATIC AND GAMETIC CHROMOSOMES IN *ROSA*.

- a.* Somatic chromosomes of *R. indica* L. Diploid 14.
- b.* Somatic chromosomes of *R. provincialis* Ait. Triploid 21.
- c.* Somatic chromosomes of *R. gallica* L. Tetraploid 28.
- d.* Somatic chromosomes of *R. canina* L. Pentaploid 35.
- e.* Somatic chromosomes of *R. Moyesii* Hemsl. and Wils. Hexaploid 42.
- f.* Somatic chromosomes of *R. Hilliana* Hurst. Octoploid 56.
- g.* Equal Gametic chromosomes of *R. indica* L. Diploid 7 ♀ + 7 ♂
♂ Diakinesis with 7 pairs of chromosomes.
- h.* Equal Gametic chromosomes of *R. Moyesii* Hemsl. and Wils. Hexaploid 21 ♀ + 21 ♂
Pollen-grain with 21 chromosomes.
- i.* Equal Gametic chromosomes of *R. Hilliana* Hurst. Octoploid 28 ♀ + 28 ♂
♀ Diakinesis with 28 pairs of chromosomes.
- j.* Unequal Gametic chromosomes of × *R. Goethe* Hort. Triploid 14 ♀ + 7 ♂
♀ Interkinesis with 14 micropylar and 7 chalazal chromosomes.
- k.* Unequal Gametic chromosomes of *R. pomifera* Herrm. Tetraploid 21 ♀ + 7 ♂
Pollen-grain divisions with 7 chromosomes.
- l.* Unequal Gametic chromosomes of *R. Fræbelii* (Christ). Pentaploid 28 ♀ + 7 ♂
♀ Late Diakinesis with 7 pairs and 21 single chromosomes.

FIG. 170. CHROMOSOMES IN *ROSA*, WORKING IN SEPTETS.

- a.* ♂ Pre-diakinesis with 7 pairs of chromosomes in the diploid *R. indica* L.
- b.* Later stage, the chromosomes with linin connections.
- c.* ♂ Pre-diakinesis with 7 pairs of chromosomes in the diploid *R. Willmottiae* Hemsl.
- d.* Later stage, the chromosomes with linin connections.
- e.* ♂ Pre-diakinesis with 7 pairs of chromosomes in three stages, in the diploid *R. indica* L.
- f.* Pollen-grains with 7 chromosomes in male nuclei (dividing) in the diploid *R. rugosa* Thunb.
- g.* ♂ Diakinesis with 7 pairs of chromosomes (cut cell) and 7 retarded single chromosomes with linin connections in the triploid *R. semperflorens* Curt.
- h.* Later stage with 7 pairs and 7 single chromosomes (cut cell).
- i.* ♀ Heterotype metaphase with 7 pairs on equatorial plate and 7 single chromosomes at the micropylar end in the triploid \times *R. Gæthe* Hort.
- j.* Somatic telophase with 7 chromosomes lagging on the equatorial plate after division in the tetraploid *R. damascena* L.
- k.* ♂ Heterotype metaphase (polar view) with 7 pairs in centre and 21 single chromosomes grouped around in the pentaploid *R. Fræbelii* (Christ).
- l.* ♂ Heterotype early telophase with paired septets reduced and 21 single chromosomes lagging on the equatorial plate in the pentaploid *R. Fræbelii* (Christ).
- m.* Later stage, the reduced septets distinguished by their more advanced condition (in this pentaploid the single chromosomes do not split).

FIG. 171. CASES OF THE LOSS OF A SEPTET IN SOMATIC CELLS OF *ROSA*.

- (a) Somatic prophase with 21 chromosomes in the (CDD) triploid in which a septet of chromosomes has been excluded from the nucleus.
- (b) A later stage in the same triploid.
- (c) Somatic plate in the same triploid with a septet of chromosomes detached from the others.
- (d) Somatic telophase in the same triploid in which a septet of chromosomes has been excluded from the division and appears to be degenerating in the cytoplasm.
- (e) Somatic prophase with 21 chromosomes in the (AAA) triploid *R. semperflorens* Curt. in which a septet of chromosomes is being excluded from the nucleus.
- (f) Somatic plate in the same triploid with a septet of chromosomes detached from the others.

FIG. 172. CHROMOSOMES IN *ROSA* WORKING IN SEPTETS IN EMBRYO-SAC MOTHER-CELLS OF IRREGULAR POLYPLOID SPECIES, SHOWING UNEQUAL REDUCTION.

- (a) ♀ Heterotype metaphase with 14 pairs of chromosomes (two double septets AACC) on the equatorial plate (2 pairs already reduced), and 14 single chromosomes (two single septets BD) towards the micropylar pole, in the irregular hexaploid (AABCCD).
- (b) ♀ Heterotype telophase in the (AACCDE) irregular hexaploid *R. alba* L. with 28 chromosomes at the micropylar pole (ACDE) and 14 at the chalazal pole (AC), leading to the formation of ♀ gametes with 28 chromosomes (ACDE) instead of 21 as in the regular hexaploids.
- (c) ♀ Heterotype metaphase with 7 pairs of chromosomes (one double septet EE) on the equatorial plate and 21 single chromosomes (three single septets ACD) at the micropylar pole (cut cell) in the (ACDEE) pentaploid *R. Fræbelii* (Christ).
- (d) ♀ Heterotype telophase in the same pentaploid with 28 chromosomes (ACDE) at the micropylar pole (cut cell) and 7 (E) at the chalazal pole, leading to the formation of ♀ gametes with 28 chromosomes (ACDE).
- (e) ♀ Interkinesis in the same pentaploid with 28 chromosomes (ACDE) in the micropylar nucleus and 7 (E) in the chalazal nucleus (two cuts).
- (f) ♀ Homotype division in the pentaploid (AABCD), the micropylar cell in metaphase with 28 chromosomes (ABCD) splitting (cut cell), the chalazal cell in telophase with 7 chromosomes (A) at each pole.

The above figures are reductions of camera lucida drawings made with Zeiss apochromatic objective 1.5 mm. and Zeiss 18 compensating ocular, using tube-length 175 mm. and Watson's Holooscopic Oil-immersion Condenser with aperture 1.34.

FIG. 173. THE FIVE DIPLOID SPECIES OF *ROSA* SHOWING DIFFERENTIAL SEPTET CHARACTERS (AA—EE).

- AA Species (a) *R. indica* L.; (b) *R. Brunonii* Lindl.; (c) *R. multiflora* Thunb.; (d) *R. moschata* Mill.
 (a) Flowers, (b) Fruit, (c) Habit of Branching, (d) Surculus with leaf.
- BB Species (e) (h) *R. Willmottiae* Hemsl.; (f) *R. sericea* Lindl.; (g) *R. Hugonis* Hemsl.
 (e) Flowers, (f) Fruit, (g) Habit of Branching, (h) Surculus with leaf.
- CC Species (i—l) *R. rugosa* Thunb.
 (i) Flowers, (j) Fruit, (k) Habit of Branching, (l) Surculus with leaf.
- DD Species (m) *R. fraxinifolia* Lindl.; (n) (p) *R. pisocarpa* A. Gray.
 (m) Flowers, (n) Fruit, (o) Habit of Branching, (p) Surculus with leaf.
- EE Species (q—t) *R. macrophylla* Lindl.
 (q) Flowers, (r) Fruit, (s) Habit of Branching, (t) Surculus with leaf.

FIG. 174. DIFFERENTIAL POLYPLOID SPECIES OF *ROSA* WITH THEIR SEPTET FORMULÆ.

- (a) Tetraploid BBCC (*R. spinosissima* L.).
 (b) Tetraploid BBDD (*R. altaica* Willd.).
 (c) Hexaploid AADDEE (*R. nutkana* Presl).
 (d) Hexaploid AABBEe (*R. Moyesii* Hemsl. and Wils.).
 (e) Octoploid BBCCDDEE (*R. acicularis* Lindl.).
 (f) Octoploid BBCCDDEE (*R. acicularis* Lindl.).

FIG. 175. GEOGRAPHICAL DISTRIBUTION OF THE DIPLOID AND POLYPLOID SPECIES OF *ROSA*.

- The figure 2 on the map represents diploid species.
 The figure 4 on the map represents tetraploid species.
 The figure 5 on the map represents pentaploid species.
 The figure 6 on the map represents hexaploid species.
 The figure 8 on the map represents octoploid species.

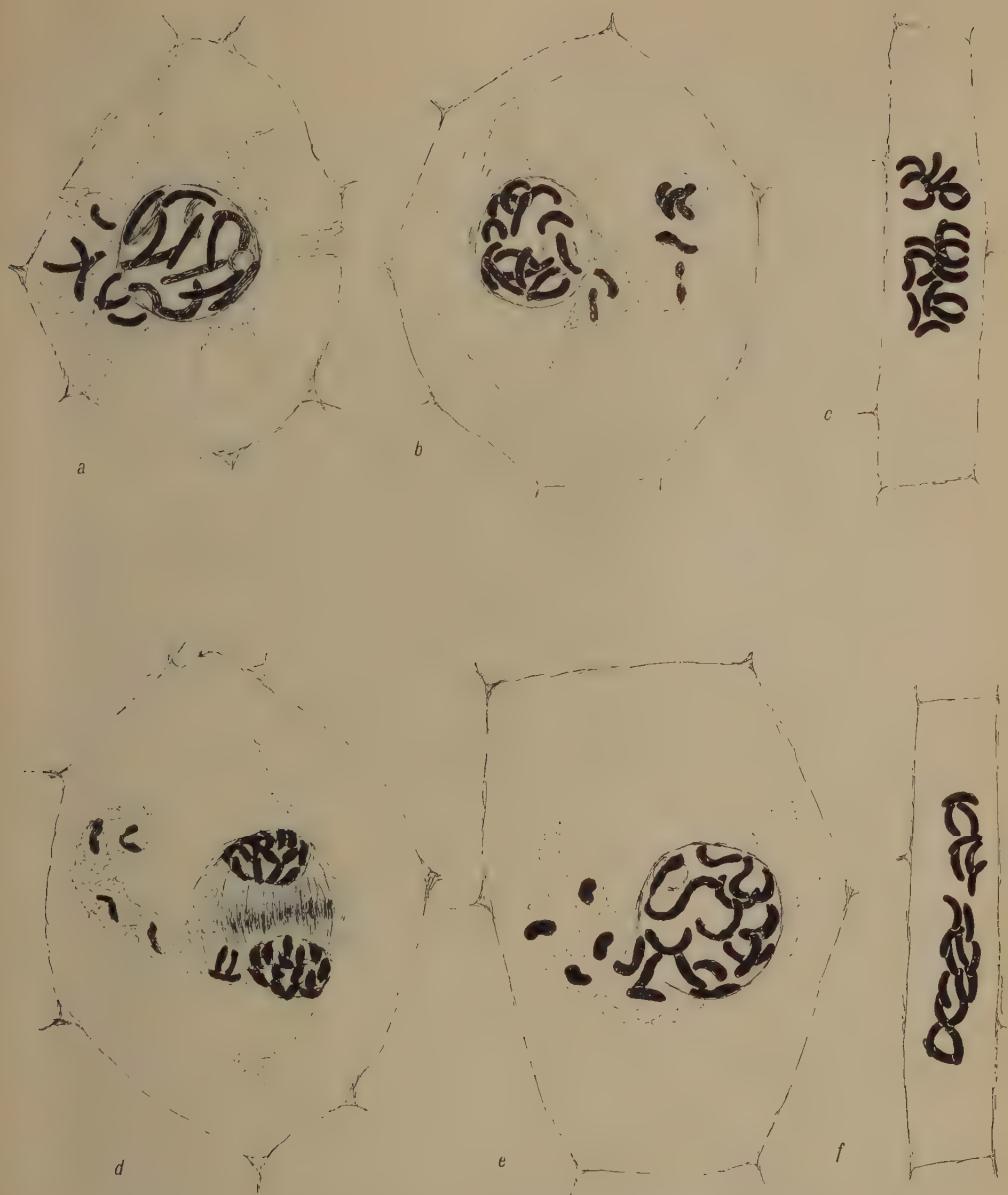
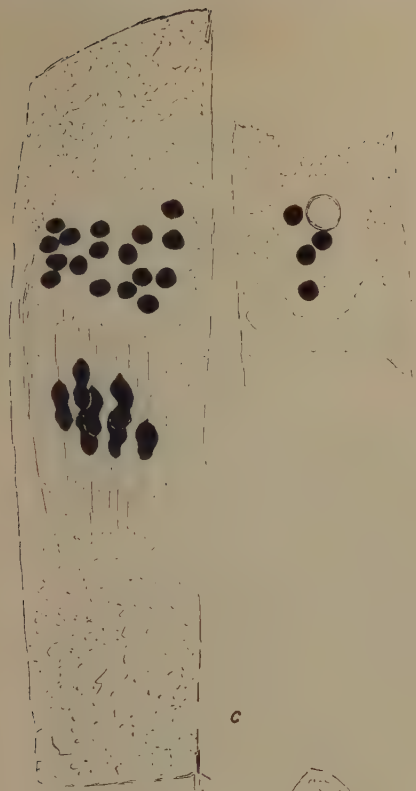


Fig. 171. Cases of the Loss of a Septum in Somatic Cells of *Rosa*. (See also fig. 170 j.)



Fig. 172. Chromosomes in *Rosa* working in Septets in Embryo-sac Mother-cells of Irregular Polyploid Species, showing Unequal Reduction.



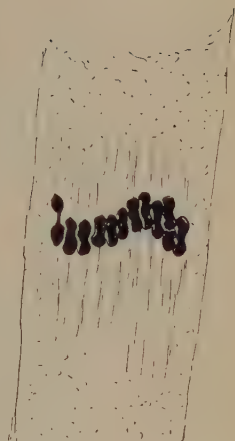
c



e



f



AA

a

b

c

d

BB

e

f

g

h

CC

i

j

k

l

DD

m

n

o

p

EE

q

r

s

t

Fig. 173. The Five Diploid Species of *Rosa*, showing Differential Septet Characters (AA—EE).



Fig. 174. Differential Polyploid Species of *Rosa* with their Septet Formulae.



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